



## Mechanisms of egg recognition in brown-headed cowbird hosts: the role of ultraviolet reflectance



Virginia E. Abernathy\*, Brian D. Peer

Department of Biological Sciences, Western Illinois University, Macomb, IL, U.S.A.

### ARTICLE INFO

#### Article history:

Received 13 March 2015  
Initial acceptance 18 May 2015  
Final acceptance 20 July 2015  
Available online  
MS. number: A15-00208R

#### Keywords:

brood parasitism  
brown-headed cowbird  
coevolution  
egg recognition  
egg rejection  
*Molothrus ater*  
UV reflectance

One of the most effective adaptations to counter avian brood parasitism is rejection of the parasitic egg, yet relatively few hosts reject eggs of the brown-headed cowbird, *Molothrus ater*. Studies have demonstrated that ultraviolet (UV; 300–400 nm) reflectance of eggs plays a role in egg rejection by hosts of parasitic cuckoos *Cuculus* spp. Only two studies have experimentally tested whether a cowbird host utilizes UV light when making egg rejection decisions, and those studies found no evidence that UV light was a significant factor. We experimentally blocked the UV reflectance of one host egg in the clutches of three rejecter species: brown thrasher, *Toxostoma rufum*, American robin, *Turdus migratorius*, and grey catbird, *Dumetella carolinensis*, to determine whether they utilize UV reflectance when rejecting eggs. We also measured the UV reflectance of each species' eggs. All host species rejected more of their own UV-blocked eggs than they did control eggs, but brown thrashers were significantly more likely to reject their own UV-blocked eggs than were American robins and grey catbirds. Brown thrasher eggs also reflected significantly more UV light than both American robin and grey catbird eggs. Our results coupled with those from similar studies suggest that hosts with brighter UV-reflecting eggs should be more likely to reject UV-blocked eggs than hosts with duller UV-reflecting eggs. This is the first study to demonstrate that UV reflectance is a parameter used by hosts of the brown-headed cowbird when rejecting eggs and further increases our understanding of the mechanisms of egg recognition in brood-parasitic hosts.

© 2015 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

One of the most enigmatic features of avian brood parasite–host coevolution is why hosts accept parasitism given its costs to their reproductive success (Davies, 2000; Rothstein & Robinson, 1998; Stokke, Moksnes, & Røskaft, 2005). Relatively few hosts of the brown-headed cowbird, *Molothrus ater*, reject cowbird eggs in spite of the often obvious difference in appearance between the host and parasitic eggs (Peer & Sealy, 2004; Rothstein, 1975, 1990). Rothstein's (1974, 1978, 1982) seminal studies demonstrated that rejecters of cowbird eggs learn the appearance of their own eggs and reject those that are sufficiently different based on background colour, spotting pattern and size (see also Lahti & Lahti, 2002; Moskát, Székely, Cuthill, & Kisbenedek, 2008; Spottiswoode & Stevens, 2010). Egg rejection may be constrained if the host and parasitic egg are similar in appearance (Peer & Sealy, 2004), if the host has intracatch egg variation that makes recognition of the parasitic egg more difficult (Peer & Rothstein, 2010) and when small-billed hosts

damage their own eggs in the process of rejecting cowbird eggs (Antonov, Stokke, Moksnes, & Røskaft, 2008; Rohwer & Spaw, 1988).

Cowbirds and their hosts have coevolved for a comparatively short time period (~2.8–3.8 million years; Rothstein, Patten, & Fleischer, 2002), which may partially explain why some of its hosts accept parasitism due to evolutionary lag (Rothstein, 1990). In contrast, the common cuckoo, *Cuculus canorus*, and its hosts have had a longer history of coevolution (6.3–8.4 million years; Rothstein et al., 2002), and as a result many cuckoo hosts have evolved rejection behaviour, which has selected for sophisticated egg mimicry by cuckoos (Davies, 2000). It has been shown that this mimicry extends into the ultraviolet (UV) spectrum (300–400 nm) that is invisible to humans (Cherry & Bennett, 2001), and that some cuckoo hosts utilize UV light when making rejection decisions (Honza & Poláčiková, 2008; Honza, Poláčiková, & Procházka, 2007; Poláčiková, Honza, Procházka, Topercer, & Stokke, 2007).

Whether brown-headed cowbirds have evolved mimetic eggs in the visible or UV spectrum has largely been ignored (but see Peer, Robinson, & Herkert, 2000; Underwood & Sealy, 2008). Only two cowbird hosts have been experimentally tested to determine whether UV reflectance is used to discriminate against foreign eggs, and eggs were not rejected at a significantly higher frequency when

\* Correspondence and present address: V. E. Abernathy, Research School of Biology, Bldg 44, Daley Rd, Australian National University, Acton, ACT 2601, Australia.

E-mail address: [vabernathy@sbcglobal.net](mailto:vabernathy@sbcglobal.net) (V. E. Abernathy).

their UV reflectance was blocked (Abernathy & Peer, *in press*; Croston & Hauber, 2013). The lack of studies on the similarity between cowbird and host eggs may be due to the fact that most cowbird hosts are accepters, leading to the assumption that there has been no selection on cowbirds to evolve egg mimicry. However, numerous hosts with eggs appearing similar to cowbird eggs are more likely to eject nonmimetic eggs than cowbird eggs (Peer et al., 2000; see also Burhans & Freeman, 1997). Thus, cowbird hosts may also use differences in UV reflectance of eggs to recognize odd eggs in the nest, especially if their eggs are difficult to distinguish from cowbird eggs.

In this study we measured the spectral reflectance of the eggs of three rejecter species, the American robin, *Turdus migratorius* (hereafter 'robin'), grey catbird, *Dumetella carolinensis* (hereafter 'catbird'), and brown thrasher, *Toxostoma rufum* (hereafter 'thrasher'), whose eggs differ in colour and maculation patterns, and we tested whether UV reflectance is a parameter used by these cowbird hosts when rejecting eggs by reducing the UV reflectance of the hosts' own eggs.

## METHODS

### Field Experiments

Robin, catbird and thrasher nests were found throughout McDonough County, Illinois and Scott County, Iowa, U.S.A. from 2009 to 2011. Robins lay light blue eggs that average  $28 \times 20$  mm, catbirds lay greenish blue eggs averaging  $23 \times 17$  mm, and thrashers lay eggs with dull white backgrounds heavily covered with reddish-brown spots averaging  $26 \times 19$  mm (Baicich & Harrison, 1997). Each nest was placed into one of two treatments: (1) one host egg was covered with UV-block, or (2) one host egg was covered with Vaseline<sup>®</sup> as a control. We used Coppertone Water Babies Sunscreen Lotion Quick Cover Spray<sup>®</sup> with 3% avobenzone as the UV-block and Vaseline Deep Moisture Creamy Formula Petroleum Jelly Cream<sup>®</sup> for the control. Avobenzone effectively blocks UV light, without changing the visible spectrum (Jou, Feldman, & Tomecki, 2012). Creamy Vaseline is of a similar consistency, but does not block UV light (Honza & Poláčiková, 2008). UV-block lasts between 24 and 48 h after application (Avilés, Soler, & Perez-Contreras, 2006; Avilés, Soler, Pérez-Contreras, Soler, & Møller, 2006; Honza & Poláčiková, 2008). Therefore, nests were checked and coating was reapplied every 1–2 days until the treatment was completed.

Experiments were conducted from the laying stage of the nest cycle (at least two eggs present) through early incubation. Eggs were considered rejected if they were removed from the nest and if the nest remained active after egg removal for at least 1 day, and were considered accepted if they remained in the nest undamaged for at least 5 days (Peer, Kuehn, Rothstein, & Fleischer, 2011; Rothstein, 1975). All eggs in the nest, regardless of treatment, were marked with indelible ink for identification, which allowed us to determine whether any eggs were rejected and whether any host eggs were lost or damaged during rejection attempts.

### Spectral Reflectance Measurements

Single eggs were randomly removed from host nests to measure their spectral reflectance before and after application of the UV-block or Vaseline ( $N = 5$  eggs per treatment). Spectral reflectance was measured using a USB4000 Ocean Optics spectrometer with a PX-2 xenon light source and a WS-1-SL white reflectance standard. The light probe had a diameter of 0.4 mm, was held inside a probe holder at a 45° angle, and was placed directly onto the surface of the egg. SpectraSuite 2008 software was used to collect the data (Ocean Optics, Dunedin, FL, U.S.A.). We divided eggs into three

regions: cap, middle and blunt end, and took three measurements in random areas within each egg region (Honza & Poláčiková, 2008). For thrasher eggs, we did not distinguish between ground colour and spotting colour when taking measurements because thrasher eggs tend to be finely spotted over the entire egg. Both robin and catbird eggs are immaculate with no spotting. Prior to measuring each region of an egg, we took a light and dark reference (three total light and dark references for each egg) to account for drifting in the spectrometer and ensure more accurate results. All measurements were taken under a black cloth in the dark to reduce noise from ambient light (Underwood & Sealy, 2008). For statistical analyses, we used an average of the nine measurements for each egg before and after coating was applied.

Spectral reflectance for each egg was recorded from 300 to 700 nm. We calculated the brightness (total amount of reflectance) in each colour spectrum (UV: 300–400 nm; blue: 400–475 nm; green: 475–550 nm; yellow: 550–625 nm; red: 625–700 nm) and total egg brightness (total amount of reflectance from 300 to 700 nm) to determine whether UV-block significantly decreased brightness in the UV range without affecting brightness in the remaining colour spectra (Honza & Poláčiková, 2008). We also used brightness values to compare egg appearance between species.

For each species, we calculated just noticeable differences (JNDs) between eggs before and after application of UV-block and then compared these JNDs between species to determine whether eggs with UV-block were more distinguishable from eggs without UV-block in one species compared to the others. JNDs represent how distinguishable one egg is from another on the basis of its spectral reflectance and the type of visual system being used in the analysis (Avilés, 2008; Cassey, Honza, Grim, & Hauber, 2008). The higher the JND value, the more distinguishable the two egg colours should be from one another. JNDs were calculated using the pavo package (Maia, Eliason, Bitton, Doucet, & Shawkey, 2013) in the R statistical package (R Core Team, 2014) using the ultraviolet-sensitive visual system (UVS) known in blue tits, *Cyanistes caeruleus*, as the UVS system was found in catbirds and robins (Aidala et al., 2012) and within the Mimidae family (Ödeen, Håstad, & Alström, 2011), of which the thrasher is a member.

We used pavo to smooth all spectra using loess smoothing (Cleveland & Devlin, 1988; Maia et al., 2013). We first determined the optimal smoothing parameter (span) to be 0.1 and applied this to all the spectra. In addition, spectra of eggs after UV-block had been applied contained negative percentage reflectance values in the 300–400 nm wavelength range. As negative percentages are uninterpretable, we transposed all spectra up by the lowest negative value so spectral curves and distances between different spectra remained the same (Maia et al., 2013).

### Statistical Analyses

We used a binomial generalized linear model (GLM) with a logit link function to determine which variables predicted rejection response. Rejection response was modelled as a binomial response variable (1 = rejection, 0 = acceptance). Independent variables included host species (robin, thrasher or catbird) experimental treatment (UV-block or Vaseline), nesting phase when the experiment started (laying or incubation) and the estimated time of laying (early season: 1 April–15 May, mid-season: 16 May–15 June, late season: 16 June–31 July). We used three categories for estimated time of laying because exact laying dates were unknown for some nests, but could be estimated based on when chicks hatched or the number of days nests were observed in the egg phase and known incubation length. We used Fisher's exact tests to compare rejection frequencies between hosts and treatments. To ensure normality of the spectral reflectance data, we performed 75

Download English Version:

<https://daneshyari.com/en/article/8489563>

Download Persian Version:

<https://daneshyari.com/article/8489563>

[Daneshyari.com](https://daneshyari.com)