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Letter

The perceptual and chemical bases of egg discrimination in communally nesting greater anis *Crotophaga major*

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The eggshells of communally breeding greater anis *Crotophaga major* consist of a blue-green pigmented calcite matrix overlaid by a chalky white layer of vaterite, both of which are polymorphs of calcium carbonate. The white vaterite layer is intact in freshly laid eggs and may function in protecting the eggs from mechanical damage, but it also abrades during incubation to reveal the blue calcite shell underneath. Previous research has shown that this color change serves a visual signaling function: nesting greater anis can discriminate between eggs that are freshly laid and those that have already been incubated, which allows them to reject asynchronous eggs laid by extra-group parasites. Here we use avian visual modeling and pigment extraction to assess the perceptual and chemical bases of such egg recognition. We found that there was no overlap between the avian perceptual space occupied by ani eggshells with and without vaterite, and that vaterite lacked both of the pigments found in the eggshell's calcite matrix, bililverdin and protoporphyrin. The visual contrast between the unpigmented vaterite and the blue-pigmented calcite appears to pre-date the evolution of the signaling function, since the related guira cuckoo *Guira guira*, also a communal breeder, lays similarly structured and pigmented eggs but does not use the visual contrast as a signal to detect parasitism.

Keywords: brood parasitism, egg recognition, Culiculidae

Introduction

To avoid caring for the offspring of unrelated brood parasites, many bird species have evolved sophisticated perceptual and cognitive abilities to recognize foreign eggs and remove them from the nest (Davies 2000). Accordingly, host species parasitized by interspecific brood parasites (such as cuckoos *Cuculus* spp. and cowbirds *Molothrus* spp.) are frequently able to reject parasitic eggs based on differences in eggshell color and patterning (Hauber et al. 2015). However, egg discrimination is much more

difficult for birds parasitized by members of the same species, since eggs laid by conspecifics tend to be very similar in size and appearance (Samas et al. 2014). Egg recognition is also rare in communally nesting bird species, in which several females lay their eggs into a shared nest and cooperatively provide parental care for the mixed clutch (Gibbons 1986, Grieves and Quinn 2018). This leaves communal nesters vulnerable to non-cooperative conspecific females, who lay their eggs into a group's nest but provide no parental care (Riehl 2013).

Tropical cuckoos in the genera *Crotophaga* and *Guira* (subfamily Crotophaginae) are communal breeders. In all four species in this clade, several pairs lay their eggs into a single nest and all of the group members participate in incubation, food delivery, and defense of the shared clutch (Riehl 2011, 2012). Reproductive synchrony in the breeding group is enforced by a unique behavioral mechanism: prior to laying her own first egg in the communal nest, each female ejects any eggs that have already been laid by her fellow group members. After she lays her own first egg, she stops removing eggs. As a result, eggs can accumulate in the nest only when all of the females in the nesting group have begun to lay. This ensures that female group members must be in reproductive synchrony, and it prevents any one female from monopolizing reproduction in the shared clutch (Riehl and Jara 2009).

Conspecific brood parasitism, in which extra-group females lay eggs into the nest of a host group but provide no parental care, is a common alternative reproductive tactic in all four species of these communally breeding cuckoo (Vehrencamp and Quinn 2004). Recent evidence suggests that one of these species, the greater ani *Crotophaga major*, is able to discriminate between parasitic and non-parasitic eggs based on visual cues associated with the timing of laying. Freshly laid eggs are covered in a white, chalky coating of vaterite, a thermodynamically unstable polymorph of calcium carbonate (Portugal et al. 2018); calcite, another polymorph of calcium carbonate, makes up the predominant component of the eggshell matrix itself (Igic et al. 2011). This fragile white layer gradually abrades away to reveal the underlying blue-green calcite eggshell (Riehl and Jara 2009). The process of abrasion begins immediately after laying – scratches are often visible within 24 h – and accelerates rapidly after incubation begins. As a result, incubated eggs appear noticeably less chalky than freshly laid eggs, and blue patches are often visible after 2–3 d of incubation.

Genetic identification of eggs has shown that extra-group parasites often lay asynchronously with respect to the host group (typically after all the hosts have finished laying), and experimental evidence suggests that hosts can recognize and remove eggs that appear to be asynchronously laid (i.e. those with the white vaterite coating still intact) (Riehl 2010a). The probability of detection increases with the degree of asynchrony, and the majority of eggs that are laid more than 3 d after the onset of incubation are removed by the host group (Riehl 2010a). Due to hatching asynchrony, these late-laid eggs often fail to hatch even when they remain in the host nest. However, having supernumerary eggs in the nest is still costly to hosts because hatching rates decrease with increasing clutch size, such that the presence of a parasitic egg (even if non-viable) reduces the probability that hosts' own eggs will hatch (Riehl and Jara 2009, Riehl 2010a).

This shell complex – a blue calcite matrix covered with a white vaterite layer – is ancestral in the cuckoo subfamily Crotophaginae and is shared by *Crotophaga* and *Guira* (Hauber 2014). The other species in this clade are not known to use the appearance of the shell as a visual cue to reject extra-group parasitic eggs (Grieves and Quinn 2018); rather, recent evidence suggests that the vaterite layer may play a role in mechanical protection, strengthening the shell and reducing the risk of fracture in large communal clutches (Portugal et al. 2018).

Previous experimental work demonstrated that the presence or absence of the white vaterite coating is the direct cue used by greater anis to recognize asynchronous eggs (Riehl 2010a). In this study, we investigated the proximate perceptual and chemical bases of this recognition cue. Our goals were: a) to determine how the color differences between the blue calcite and white vaterite are perceived by the ani visual system (presumed to be violet-sensitive, as shown for other Cuculiformes; Aidala et al. 2012), and b) to identify the shell pigments responsible for these differences. We used spectrophotometry to quantify the avian-perceivable spectral reflectance of the vaterite and the eggshell matrix, and visual modeling (Cassey et al. 2008) of the cuculid color vision system to quantify the perceptual space occupied by the calcite and vaterite layers (Stoddard and Prum 2008). Note that this approach did not analyze the ani's perception of the complex pattern generated by the abraded white vaterite layer against the blue background shell coloration. We then used ultra-high performance liquid chromatography (UHPLC) (Verdes et al. 2015) to assess the presence of the two primary pigments found in avian eggshells, biliverdin and protoporphyrin (Hanley et al. 2015), in the vaterite and calcite layers of the greater ani eggshell. Finally, as a phylogenetic comparison, we also analyzed the pigment composition of eggshells of the closely related guira cuckoo (Sorenson and Payne 2005). Like the greater ani, the guira cuckoo nests communally and lays blue-green eggs initially covered incompletely with blotches of white vaterite coating; however, this species is not known to reject conspecific eggs after females began to lay their own eggs in the clutch (Cariello et al. 2004).

Methods

Egg sampling

Freshly laid greater ani eggs were collected and destructively sampled from a nesting population in the Barro Colorado Nature Monument, Panama (9.1521°N, 79.8465°W; under Smithsonian Tropical Research Inst. IACUC protocol 2015-0601-2018 to CR). Anis nest in forested areas along lakes, rivers, and other bodies of fresh water; the open-cup stick nests are typically placed in emergent vegetation in the water

or in overhanging branches near the water's surface (Riehl and Jara 2009). Eggs were collected during July 2016. The eggs were collected from different communal nests, thus representing a source of different individual females.

Freshly laid captive guira cuckoo eggs were collected by zoo staff at the Wildlife Conservation Society's Bronx Zoo facility, also in 2016; the eggs were sourced from a communal nest attended by several females. We did not conduct genetic analyses of individual eggs in either species.

Perceptual analysis

We used reflectance spectrophotometry to objectively measure variation within and between eggshell surfaces with vaterite intact and removed. From each egg, we manually removed a small (ca 10 mm^2) amount of vaterite using a Kimwipe and molecular grade water. This method has been shown to remove the vaterite without altering the calcite layer beneath (Portugal et al. 2018). To measure spectral reflectance, we used an Ocean Optics Jaz UV-VIS spectrometer with a QR400-7-SR UV-VIS probe and a PX pulsed xenon light source. The probe tip was mounted in a rubber sheath to exclude ambient light adjusted so the probe tip was 3 mm from the egg surface. Three reflectance measurements were taken for each egg at different points within both the vaterite intact and removed areas. The probe was recalibrated against a white standard (Ocean Optics WS-1) after each egg. We trimmed the curves to the avian visible spectrum (300–700 nm) and averaged the three reflectance curves to produce one curve representing reflectance of the vaterite intact and removed area of each egg. Our experimental removal of vaterite was not intended to mimic the extent of abrasion on a naturally incubated egg; rather, our aim was to quantify the extent to which the reflectance spectra of vaterite and calcite overlap in the avian perceptual space, in order to test the hypothesis that the contrast is sufficient to be used as a recognition cue.

To compare colors accounting for the spectral sensitivity of the avian visual system, we used the program pavo (Maia et al. 2013), which analyzes reflectance curves by modeling how they stimulate the four cones of the avian retina, and plots each color as a point in tetrahedral color space. The greater ani, as a member of the Cuculidae family, likely shares a violet-sensitive (VS) visual system with the long-tailed cuckoo *Urodynamis taiteensis* (Aidala et al. 2012), and so we analyzed the spectral data using the average avian violet-sensitive (VS) spectral sensitivity curve (Endler and Mielke 2005). We plotted the average reflectance curves and their standard deviations for eggs with vaterite intact or removed. We then used the relative cone stimulation values from pavo to project each set of color reflectances as a point in the tetrahedral avian perceivable color space (Stoddard and Prum 2008). We ran the analyses under both open canopy and forest shade illumination conditions (Stoddard and Prum 2008) to account for variation in the greater ani's preferred nesting habitat (typically in shoreline vegetation overhanging the water, which can range from partly shaded to completely

open). We applied the function 'voloverlap' in pavo to quantify potential overlap in color space between the colors of eggs with vaterite intact and removed under both illumination conditions. This is done by first calculating the tetrahedral volume occupied by each set of points in color space, and then calculating the overlap between them.

Chemical analyses

For the pigment analysis, we used an ethylenediamine-tetraacetic acid (EDTA) extraction protocol (detailed by Gorchein et al. 2009, as applied in Verdes et al. 2015). We used the same instrumentation and analysis methods as detailed in previous eggshell pigmentation work to extract biliverdin and protoporphyrin IX (Verdes et al. 2015, Dearborn et al. 2017). The protocol was universally applied to each fragment, ranging between 200 and 500 mg of weight.

The EDTA extraction protocol results in 1 ml of dissolved sample in acetonitrile-acetic acid (4:1 v/v). We used a Cary 300 UV-Vis spectrophotometer to measure samples for their UV absorbance. Biliverdin peaks were observed at 377 nm while protoporphyrin absorbance was observed at 405 nm (Igic et al. 2010, Verdes et al. 2015).

Samples were also analyzed using an Agilent System UHPLC. Samples were run with a flow rate of 0.40 ml min^{-1} using water with 0.01% formic acid and acetonitrile with 0.1% formic acid as solvents A and B, respectively. The linear gradient was set to 2% A and 98% B at 6.5 min. Absorbance was measured at 377 and 405 nm. Biliverdin peaked at ~3.5 min with protoporphyrin observed at ~5.6 min (Fig. 1). Pigment presence or absence was also confirmed through mass spectrometry (Verdes et al. 2015). We used Beer Lambert's law ($A = \epsilon bc$) to calculate pigment concentration and to standardize samples by eggshell weight.

Vaterite removed from the eggshell exterior was tested separately with the same methodology. Vaterite samples from the same corresponding eggshell fragments weighed between 6.40 and 10 mg. Due to the apparent hydrophobic properties of the substance, it did not easily dissolve and, upon storage in a 4°C fridge, it precipitated out of the acetonitrile solution. For this reason, we recommend developing an alternative to the Gorchein et al. (2009) protocol in future work for analyzing vaterite in mass spectrometry systems.

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.9043m48> (Hauber et al. 2018).

Results

Perceptual analysis

Eggs (n = 22) with or without vaterite showed distinct reflectance curves, with the vaterite curve highly reflective and flat in the visible range (400–700 nm), and the calcite curve
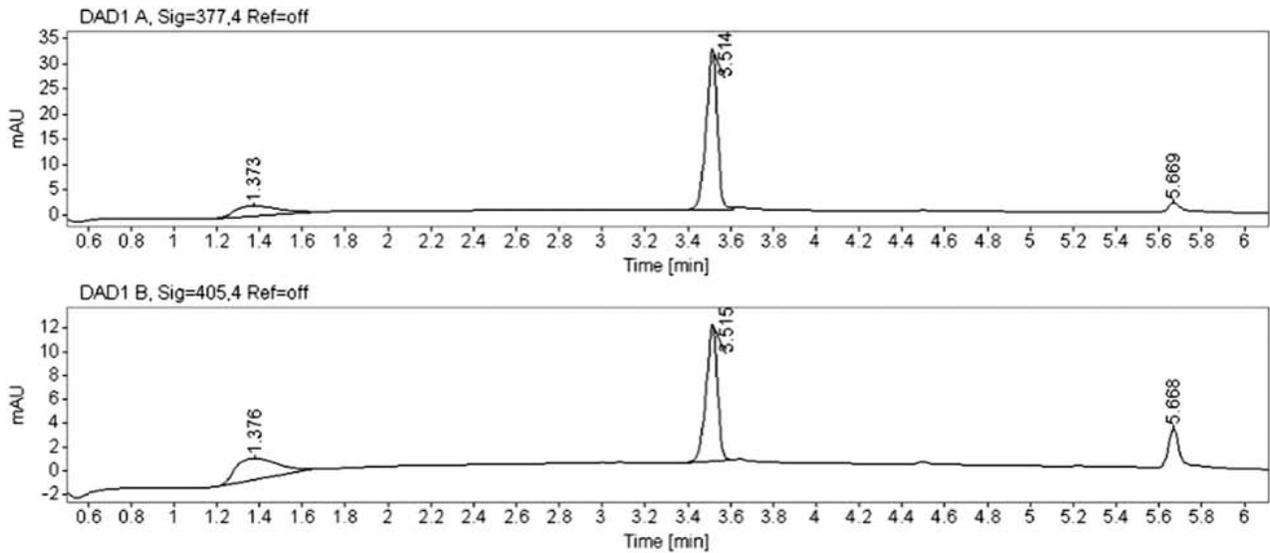
Figure 1. Representative ultra-high performance liquid chromatography (UHPLC) traces of biliverdin (3.5 min) and protoporphyrin IX (5.6 min) presence in the vaterite-free eggshells of guira cuckoos.

showing a peak in both UV and blue-green wavelengths (Fig. 2). Analysis of these data from the VS avian visual system revealed that there was no overlap between the avian perceptual spaces occupied by eggshells with and without vaterite, in either open canopy or forest shade illumination (Table 1).

Chemical analyses

The chemical analyses detected no biliverdin or protoporphyrin from the vaterite layer of the eggshells of either greater anis (n = 10) or guira cuckoos (n = 6). In contrast, both pigments were detected in the calcite layer of both species' eggshells. Biliverdin was detected in all samples of both species (mean ± SD greater ani: 4.51 ± 1.56, guira cuckoo: 2.88 ± 0.43), whereas protoporphyrin was detected in only 1 of 10 greater ani (0.23) and in all 6 of 6 guira cuckoo (0.12 ± 0.05) eggs.

Discussion

Rejecters of avian brood parasitism use multiple cues to recognize and reject parasitic eggs, which can include background
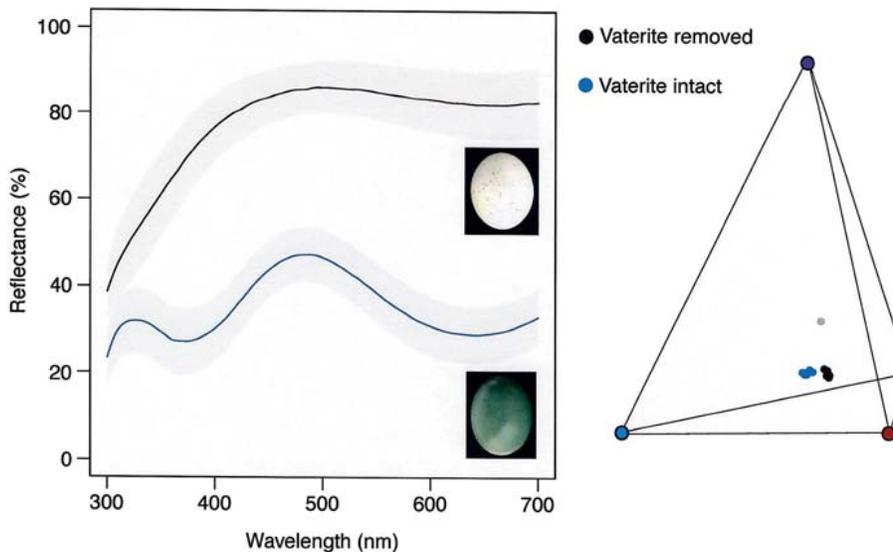
Figure 2. The average (solid lines) and standard deviation (shaded area) of the avian-visible reflectance curves for 22 greater ani eggs shown with vaterite intact (black) and removed (blue). The visualization of the resulting colors in the average avian violet-sensitive color space indicates no overlap between the color spaces. Open canopy nest illumination conditions are visualized here; the conclusions are qualitatively the same for under forest shade illumination conditions (Table 1).

Table 1. Relative color volume and percent overlap between the colors of eggs with vaterite intact or removed under two nest illumination conditions.

Illumination conditions	Color volume (vaterite intact)	Color volume (vaterite removed)	Color volume overlap (%)
Open canopy	3.08×10^{-7}	2.32×10^{-6}	0
Forest shade	1.29×10^{-7}	1.15×10^{-6}	0

color (Hanley et al. 2017), pattern (Stoddard et al. 2014), and shape (Segura et al. 2016). The salience of these cues, and their relative importance to the receiver, must depend on their reliability and availability. In bright light levels, for example, contrast in color (as perceived by a bird's eye) is often the salient cue, whereas differences in luminance or patterning may be used in low light levels, or when the color of the parasitic egg is indistinguishable from that of the host egg (Spottiswoode and Stevens 2012). The analyses in this study suggest that, to the presumably violet-sensitive greater ani visual system, the contrast between the blue calcite and white vaterite colors should be distinguishable even at low light levels, such as in a shaded nest; the areas occupied by the two colors do not overlap at all in the ani perceptual space (Fig. 2). This result supports previous experimental work suggesting that, in this species, the extent of the vaterite coating on the egg is a predictable trait indicating its age, and, by extension, a reliable cue indicating whether it was laid by a group member or an extra-group parasite (Riehl et al. 2015). Egg size and shape are not reliable cues of maternity in either the greater ani (Riehl 2010b) or the related guira cuckoo (Cariello et al. 2004), and the pattern of the vaterite abrasion is likely not consistent for individual females. We did not, however, explicitly test avian pattern perception in our visual modeling approach (Stoddard et al. 2014).

Chemical analyses here also revealed the presence of two classes of tetrapyrrole pigments (Hanley et al. 2015) in the eggshells of greater anis and guira cuckoos. Biliverdin, which is responsible for blue-green pigmentation, was found in the shells of both species, whereas protoporphyrin, which results in reddish or brownish coloration, was found consistently only in guira cuckoo eggshells. These two pigments are ubiquitous in birds and are evolutionary conserved, producing the entire range of eggshell colors in extant and extinct birds (Igic et al. 2010, Hanley et al. 2015).

Within the cuckoo family (Cuculidae), eggshell appearance is unusually labile, with a striking diversity of coloration and patterning across species (and, in the case of the common cuckoo *Cuculus canorus*, within species; Stoddard and Hauber 2017). In the clade containing the New World ground-cuckoos and the anis, blue-green coloration has likely arisen at least twice independently in this clade: in the crotophagine lineage (*Crotophaga* and *Guira*), and in the striped cuckoo *Tapera naevia* (Hauber 2014). The latter species is an obligate interspecific brood parasite, and blue-green egg coloration appears to have arisen in some populations as an adaptation to successfully parasitize hosts by mimicking their eggshell blue eggs (Mark 2013).

The potential adaptive benefits favoring blue-green egg coloration in the communally breeding crotophagine cuckoos are still unclear (Schmaltz et al. 2008), but the results of this study, as well as recent experimental work, suggest that the vaterite coating (and the resulting color, and pattern, contrasts) probably arose in this lineage for reasons unrelated to visual signaling or intraspecific brood parasitism. Given that communal clutch sizes are large in all of the crotophagine cuckoos (up to 20 eggs) and that eggs collide with substantial force when they are turned (Vehrencamp 1978), the vaterite coating may represent an adaptation to reduce the risk of shell fracture during egg-laying and incubation. In support of this hypothesis, Portugal et al. (2018) found that greater ani eggshells are unusually thick for the size of the egg, and that the vaterite coating further increases the thickness of the shell cuticle by up to 10%. The hardness and elasticity of vaterite was found to be similar to that of calcite, and the vaterite layer decreases the contact pressure on the calcite shell during impact. It is possible, therefore, that the vaterite layer was initially favored by selection on the mechanical strength of the eggshell amongst the ancestors of the crotophagine cuckoos, and that its role in visual signaling arose later in the context of conspecific brood parasitism in the greater ani. Although conspecific brood parasitism has been recorded in the other crotophagine cuckoos, its frequency and costs are poorly understood. Future research is needed to charaterize the evolutionary dynamics of host–parasite interactions in the other species in this lineage, and to determine whether similar proximate mechanisms are used to recognize and reject eggs from extra-group parasites.

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