Host Responses to Foreign Eggs across the Avian Visual Color Space

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ABSTRACT: Despite extensive research on the sensory and cognitive processes of host rejection of avian brood parasites' eggs, the underlying perceptual and cognitive mechanisms are not sufficiently understood. Historically, most studies of host egg discrimination assumed that hosts rejected a parasite's egg from their nest based on the perceived color and pattern differences between the parasite's egg and their own. A recent study used a continuous range of parasitic egg colors and discovered that hosts were more likely to reject browner foreign eggs than foreign eggs that were more blue green, even when their absolute perceived color differences from the hosts' own egg colors were similar. However, the extent of these color biases across the avian perceivable color space remains unclear. Therefore, we built on this previous study by testing European blackbirds' (*Turdus merula*) responses to model eggs spanning an unprecedented volume of the avian color space. We found that host decisions depended on avian perceived hue, saturation, and luminance of the parasite's egg; hosts generally accepted eggs that were bluer or more blue green and more often rejected eggs that were less saturated or darker. We suggest that future studies investigate the underlying mechanisms of foreign egg discrimination in other host lineages to determine the prevalence and phylogenetic conservation of such perceptual biases among birds.

Keywords: avian perception, brood parasitism, color categorization, color vision, European blackbird.

Introduction

Coevolutionary arms races are widespread in nature and represent a driving force in evolution (Dawkins and Krebs 1979). Arms races associated with brood parasitism fall into two categories: intraspecific brood parasitism and interspecific brood parasitism. Intraspecific brood parasitism occurs when an individual lays its eggs inside the nests of other individuals of the same species, and it is present in many species of insects (Field 1992), fishes (Taborsky et al. 1987), and birds (Yom-Tov 2001). Interspecific brood parasitism occurs when these relationships manifest between different species, such as between the cuckoo catfish, *Synodontis multipunctatus*, and its mouth-brooding cichlid hosts (Blažek et al. 2018). A reciprocal arms race can ensue because defense abilities of hosts select for counteradaptations in parasites to evade those defenses and vice versa (Van Valen 1973).

Avian brood parasitism is a classic example of a coevolutionary arms race between parasitic birds and their hosts (Payne 1998; Rothstein 1990; Davies 2000; Stoddard and Hauber 2017). Brood parasitism selects for host defenses against parasites because hosts that do not defend against brood parasitism may lose some or all of their offspring while investing into raising genetically unrelated young in parasitized nests (Rothstein 1990; Davies 2000; Samaš et al. 2018). Many hosts evade parasitism by one or more of a suite of adaptive defense behaviors (Feeney et al. 2014). A commonly employed strategy is to reject foreign offspring from their nests as either eggs (reviewed in Medina and Langmore 2015) or young (reviewed in Grim 2006). Because hosts tend to reject eggs that appear dissimilar to their own, they inadvertently select for parasites that lay eggs that are more mimetic (Brooke and Davies 1988; Antonov et al. 2006; Spottiswoode and Stevens 2010; Bán et al. 2013; Samas et al. 2014; Hauber et al. 2015).

With every subsequent generation, hosts engaged in such arms races can face parasite eggs that are more similar and thus more challenging to discriminate (Lahti and Lahti 2002; Spottiswoode and Stevens 2010; Stoddard et al. 2014). Nonetheless, variation in parasitic eggshell appearance can continue to provide hosts with information useful for hosts to decide whether to reject the egg, including eggshell size (Rothstein 1982; Luro et al. 2018), shape (Bán et al. 2011; Zölei et al. 2012), pattern (Spottiswoode and Stevens 2010; Stoddard and Stevens 2011), and avian-perceived color (Avilés 2008; Cassey et al. 2008).

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The majority of studies examining host egg recognition have used either a single egg model type (e.g., generic blue) or egg models of limited categories (e.g., mimetic vs. nonmimetic), which did not allow for the comprehensive assessment of host responses to eggs of varying colors (e.g., Davies and Brooke 1989; de la Colina et al. 2012; Igic et al. 2015; Liang et al. 2016). A recent study measured the responses of two congeneric host species, the American robin (*Turdus migratorius*) and the European blackbird (*Turdus merula*), to experimental eggs with colors spanning the natural avian eggshell color gamut (described in Hanley et al. 2015*b*; Canniff et al. 2018) and those with colors along a single orthogonal axis of artificial egg colors (Hanley et al. 2017). Contrary to the traditional expectation (Rothstein 1982; Stoddard and Stevens 2011; Hauber et al. 2015), this study found that host rejection decisions were not simply based on the degree of perceived similarity between the host's own egg and the foreign egg (which is not necessarily synonymous with mimicry; see Grim 2005). Instead, hosts were biased toward rejecting brown eggs, while blue-green eggs were readily accepted regardless of the absolute perceived difference from their own eggs' colors (Hanley et al. 2017; see also Dainson et al. 2017).

This experiment, and a subsequent study on the chalk-browed mockingbird (*Mimus saturninus*) that is a common host of the shiny cowbird (*Molothrus bonariensis*) in Argentina (Hanley et al. 2019*b*), illustrated that some hosts do not base decisions on perceptual distances alone. Instead, these studies suggest that an alternative decision rule may better explain how host responses may vary across the avian color space (e.g., fig. S3 from Hanley et al. 2017). Specifically, if host responses depend on perceptual distances, rejection responses should be more likely when hosts are presented with colors more dissimilar to their own; however, this was not always the case. Previous research has shown that hosts were equally likely to reject all artificial eggshell colors, and, thus, this axis of color variation was not useful in predicting whether they would reject a foreign egg model (Hanley et al. 2017). By contrast, hosts responded predictably along an axis of natural egg colors, varying their response based on an egg's particular color (e.g., acceptance of blue-green eggs and rejection of brown eggs; Hanley et al. 2017, 2019*b*). This suggests that multiple aspects of color, such as hue, saturation, and luminance, may interact and provide hosts with valuable information for egg discrimination decisions. Previous research that has examined host responses to eggs with colors spanning the avian tetrahedral color space (fig. 1*A*) have left large volumes of this color space unsampled (e.g., Bán et al. 2013; Croston and Hauber 2014; Hanley et al. 2017, 2019*b*; Manna et al. 2019). Thus, our understanding of how hosts use color information for egg discrimination is limited. Here, we experimentally manipulated the hue, saturation, and luminance of

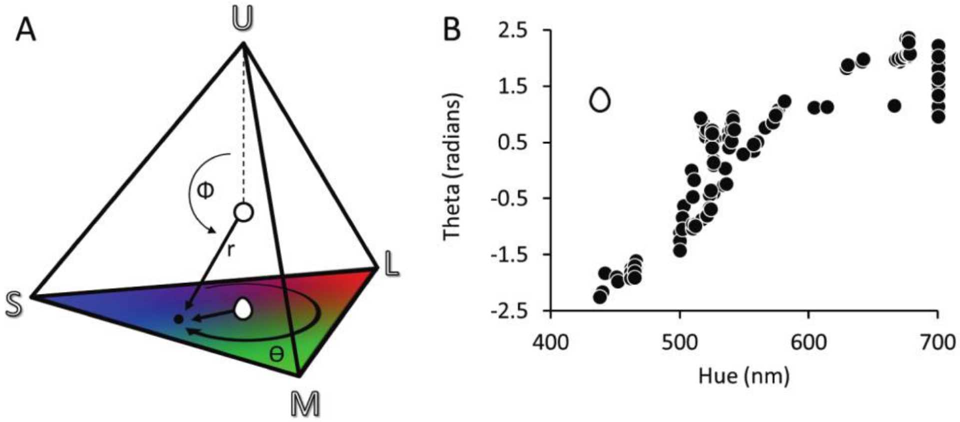

Figure 1: *A*, An avian tetrahedral color space where any stimulus (e.g., a blue-green egg, represented by a black dot) can be plotted within this space based on the relative stimulation of the ultraviolet-wavelength-sensitive (U) photoreceptors and each of the short-, medium-, and long-wavelength-sensitive (S, M, and L, respectively) photoreceptors. A stimulus's position within this space can be defined by angle θ, which represents hue and is depicted on the floor of the tetrahedron; angle Φ, which represents an additional dimension of hue undetectable to human eyes (i.e., ultraviolet variation); and saturation (r), which represents the intensity of the color from dull at the achromatic point (open circle) to intense colors (away from it). The experimental eggs used in this study reflected relatively little light in the ultraviolet range (table 1); therefore, we calculated saturation as the perceived difference between a white egg (represented by the white egg, with relatively little ultraviolet reflectance) and each experimental egg (depicted by the arrow). Instead of using θ as an estimate of hue, we calculated hue as the wavelength of peak reflectance. *B*, These two variables were related to one another, except in the case of the white egg (represented by the white egg), which does have a wavelength of peak reflectance but for which θ is not a meaningful measurement (i.e., θ measures rotations around the center, and the white egg is at the center). Data underlying this figure have been deposited in the Dryad Digital Repository (https://dx.doi.org/10.5061/dryad.q293c9g; Hanley et al. 2019*a*).

egg models across a larger avian color space than any other published study to date to determine how these aspects of color are used in egg discrimination.

Specifically, we examined the behavioral responses of the European blackbird (*T. merula*; hereafter blackbird) to variably colored, unspotted model eggs spanning a broad array of avian-perceivable colors (hues) and relative intensities (saturation). We predicted that hosts would be biased toward accepting blue-green eggs and biased toward rejecting eggs with colors dominated by reflectance of longer wavelengths, for example, oranges and browns (see fig. S3 in Hanley et al. 2017; see also Bán et al. 2013; Hauber et al. 2015). Because blackbird eggshell coloration falls close to the achromatic point in the avian color space (see fig. 2*B* from Hanley et al. 2017), we predicted that the rejection probability of model eggs would increase with increasing color saturation (i.e., increasingly vibrant and unnatural colors). Last, we predicted that luminance should be unrelated to host rejection response because blackbirds did not use achromatic information in rejection decisions in our prior experiment (Hanley et al. 2017).

Material and Methods

Study Area and Experimental Procedures

To provide thorough coverage across the avian perceivable color space, we combined our previously collected data on blackbirds ($N = 82$ nests from Hanley et al. 2017, collected in 2014) with identically collected data from a new set of experiments on blackbirds (new $N = 82$ nests, collected in 2015 and 2016; total $N = 164$ nests). We analyzed data only from nests with parents that did not desert the nest (see "Results"), which reduced our total sample size to 155 nests. Both data sets were collected in Olomouc, Czech Republic (49° 35′38″N, 17°15′3″E). The new data set was collected between March and July in 2015 and 2016. Only nonpredated nests that reached clutch completion were included in our analysis (Hanley et al. 2017). In 2015–2016 we also conducted 15 control trials, where one experimenter placed his hand over the nest for 10 s without manipulating the clutch to test whether nest desertion was a specific response to our experimental parasitism during those seasons (Hanley et al. 2015*c*). To minimize the chance of sampling the same females more than once per season, we avoided running subsequent experiments in the same breeding territories (Samaš et al. 2013; Hanley et al. 2015*c*).

We assumed that blackbird females lay one egg per day and have a 13-day incubation period (Hanley et al. 2015*c*). In this population, clutches typically contain four or five eggs (Samaš et al. 2013), and we added experimental eggs 2.13 ± 0.17 days (mean ± SE) after the last egg was laid. Similar to most other typical and potential common cuckoo (*Cuculus canorus*) hosts, blackbirds do not vary their egg rejection responses between laying and incubation stages (Grim et al. 2011 and references therein), including in our study population (Grim et al. 2014). Parental attendance at the time of experimentation can influence host rejection response (Hanley et al. 2015*d*); therefore, we also recorded the presence of the blackbird female when the experimental egg was added to her nest to statistically control for this effect. All of the experimental nests were checked daily for 6 days to determine whether the model egg was accepted or rejected or whether the clutch was deserted (following Grim et al. 2011).

Experimental Egg Models

All models were manufactured consistently by a single individual (Z. Šebestová) who was commissioned to produce eggs identical to those she had supplied for all of our blackbird studies in Olomouc and elsewhere previously (Grim et al. 2011, 2014; Samas et al. 2014; Hanley et al. 2015*c*, 2015*d*, 2017). The sizes of these egg models (mean ± SD = 22.4 × 16.9 mm, $N = 32$; data from Hanley et al. 2015*c*) were within the range of real cuckoo eggs found in the nests of common redstarts *Phoenicurus phoenicurus* (further details in Samaš et al. 2011). They were painted to cover natural eggshell color ranges (Hanley et al. 2015*b*) and unnatural color ranges (Hanley et al. 2017). However, unlike in our previous study, our current goal was to more thoroughly sample the avian color space; therefore, we constructed a color wheel containing 73 colors, based on six main hues (blue, cyan, green, yellow, red, and magenta) and white (fig. 2). Hues were mixed together at variable proportions with the next most similar hue, for example, 75% blue and 25% cyan, 50% blue and 50% cyan, and 25% blue and 75% cyan. This resulted in 24 unique hues, for which each was displayed at three distinct shades created by mixing each paint mixture with variable proportions of white, such that the hue was pure (i.e., 0% white), 25% white, or 50% white (i.e., variable saturation). In addition, we included a single white egg model representing the center of the color wheel (fig. 2). Each egg model was painted using a single unique color.

Color Measurement and Visual Models

We used a spectrometer (Jaz, Ocean Optics, Dunedin, FL) with a pulsed xenon light source (Jaz PX) and a white reflectance standard (WS-1) for reflectance spectrometry to objectively measure colors. The measurement probe of the spectrometer had an anodized aluminum sleeve at its end to maintain a consistent distance between the measurement surface and the spectrometer's fiber-optic cable. Unfortunately, during the course of our experiment, this probe tip slid slightly, thus changing the distance between the probe tip and the egg. This altered the luminance of the model eggs' color measurements, and, therefore, we instead remeasured the same paint

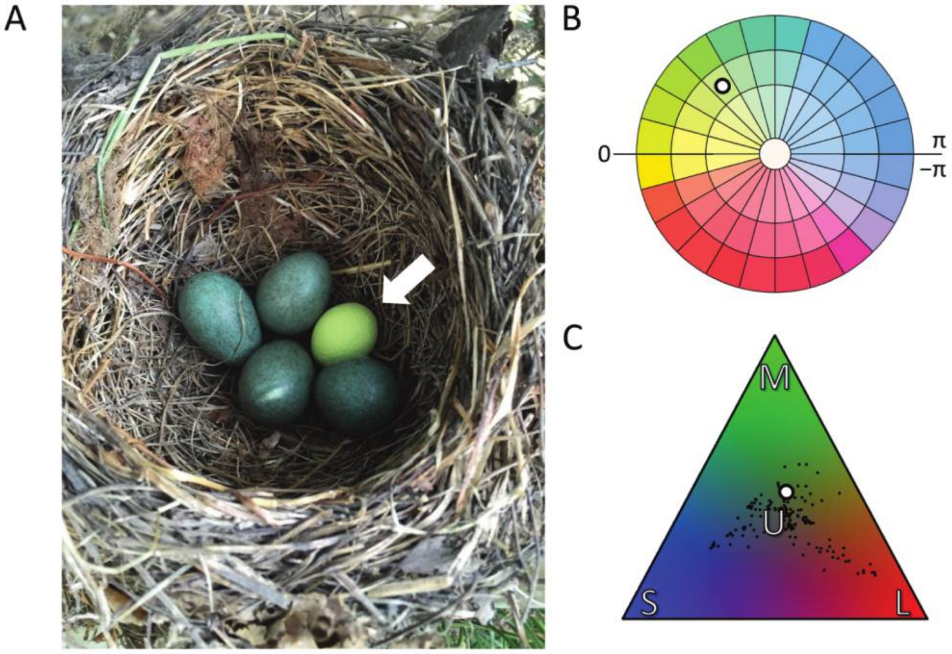

Figure 2: *A*, A European blackbird clutch with an example of the experimental egg (arrow) in a nest with four real eggs (photo credit: K.G.). This egg is depicted (as a white dot) in a color wheel (*B*) illustrating 73 colors generated for this study and in an avian tetrahedral color space (*C*; see fig. 1), here shown from above the UV vertex, depicting the distribution of experimental eggshell colors used in this study ($N = 155$). This includes novel egg colors ($N = 73$) as well as the colors of model eggs ($N = 82$) used in a previous study (Hanley et al. 2017). Hue values found around the color wheel (*B*) ranged from $-\pi$ to $+\pi$ (following Stoddard and Prum 2008). Data underlying this figure have been deposited in the Dryad Digital Repository (https://dx.doi.org/10.5061/dryad.q293c9g; Hanley et al. 2019*a*).

mixtures that were also applied to watercolor paper. We painted each color on watercolor paper 20 times and measured every color patch three times, taking the average of each color. We measured 70 of the 73 colored eggs, such that each egg was measured six times each (twice on the blunt pole, equator, and sharp pole). The colorimetric values of interest (see below) were very similar between the colors measured on the eggs and on paper (hue: $r = 0.94$, 95% confidence interval [CI] = 0.90–0.96, $N = 70$, $P < .0001$; saturation: $r = 0.85$, 95% CI = 0.77–0.91, $N = 70$, $P < .0001$; luminance: $r = 0.96$, 95% CI = 0.94–0.98, $N = 70$, $P < .0001$).

We then used the "pavo" R package (Maia et al. 2013) to process these spectra and calculate the relative sensitivity of each of the blackbirds' photoreceptors (Govardovskii et al. 2000; Hart et al. 2000), while accounting for oil droplet cutoffs (Hart and Vorobyev 2005), to make our procedures identical to those of Hanley et al. (2017). Perceived luminance was estimated using the summed response of the two longest-wavelength photoreceptors. This neural noise-limited visual model (Vorobyev and Osorio 1998; Vorobyev et al. 1998) integrates stimulus reflectance, photoreceptor sensitivity, and a standard metric of daylight illumination to generate relative quantum catch estimates. These estimates represent the extent to which two stimuli are perceivably different. These differences are calculated as just noticeable differences (JNDs), such that a value of 1 indicates that two stimuli would be just discriminable under ideal viewing conditions (larger values suggest a greater likelihood that the stimuli would be perceived as different). We quantified saturation as the JND between each colorful egg and the uncolored white egg (fig. 1*A*).

We calculated hue as the wavelength of peak reflectance (Andersson et al. 1998; Delhey et al. 2003; Smiseth et al. 2001). However, this colorimetric variable may not directly relate to avian perceived hue; therefore, it was necessary to confirm that our hue metric was related to how blackbirds might perceive hue. To do this we first transformed quantum catches into an avian tetrahedral color space (Stoddard and Prum 2008; Endler and Mielke 2005), which encompasses the range of colors visible to birds. The tetrahedral space is defined by four apexes corresponding to each photoreceptor (fig. 1), such that any color can be defined by its relative stimulation of each of the four photoreceptors. Within this space, the spherical coordinate θ represents human visible hues (range: $-\pi$ to π), while Φ (range: $-\pi/2$ to $\pi/2$) represents a second hue dimension visible to birds but not humans (i.e., ultraviolet hue). Because θ is a circular variable, we fitted a circular-linear regression using the "circular" package in R, to predict θ by the hue. Hue was positively correlated with θ of experimental eggs used in nondeserted nests ($r = 0.56$, 95% CI = 0.45–0.65, $N = 155$, $P < .0001$; fig. 1*B*) and, therefore, is a useful linear metric to describe avian perceived hue. However, no hue was within the ultraviolet (hereafter UV) range, and hue was not correlated with Φ ($r = 0.05$, 95% CI = −0.11 to 0.20, $N = 155$, $P = .57$), which we did not intentionally manipulate.

The previously collected data (Hanley et al. 2017) used a different spectrometer (but the same white standard), which has no influence on the coordinates within a color space because the tetrahedral color space lacks luminance information (Stoddard and Prum 2008) but would impact year-to-year variation in perceived luminance. Therefore, to ensure comparability between the data sets, luminance was centered and scaled within each year (Schielzeth 2010), and year was included as a covariate in all analyses. When compared with natural eggshell colors (data from Hanley et al. 2015*a*), the paints we used generated model eggs with colors that had significantly greater variance in quantum cone catch for all four photoreceptor types (table 1). Although UV reflectance was low on our model eggs, the mean UV quantum catch of these experimental eggs was similar to that calculated from real avian eggs from a large comparative data set (table 1).

Statistical Analyses

Nest desertions were unrelated to our experimental procedure (see "Results"). Therefore, we used a binomial generalized linear model to test whether the host response (either egg acceptance or rejection) was predicted by the experimental egg's hue, saturation, perceived luminance, and the interactions between these three color variables. We performed a backward stepwise elimination procedure, removing nonsignificant terms (following recommendations of Grafen and Hails 2002), to test for other potentially influential variables: clutch size (continuous; mean ± SE: 4.33 ± 0.05 eggs), whether the female was flushed from the nest (categorical; yes or no), nest age (continuous; mean ± SE: 2.14 ± 0.17 days after clutch completion), and year of the experiment (categorical; 2014, 2015, or 2016). We also included the laying date of the first egg (hereafter laying date; continuous; 1 = January 1), which we centered within each year to avoid seasonal biases (see Grim et al. 2011; Hanley et al. 2015*d*). In this study the models were not specifically designed to reflect in the UV range (e.g., Šulc et al. 2016), and we did not attempt to systematically manipulate this dimension; however, to account for decisions based on UV information, we included the quantum catch of the UV-sensitive (hereafter UVS) cone as a potential covariate (Honza et al. 2007). To aid the interpretation of individual parameters and their interactions, we centered and scaled all continuous variables prior to analyses (Schielzeth 2010). We always retained our main predictors of interest (avian perceived hue, saturation, luminance, the interactions among these variables, and year as a covariate), which we experimentally manipulated, in all steps of this selection process. We acknowledge that *P* values from such selection procedures do not account for variable selection uncertainty (Marra and Wood 2011) and, therefore, should be viewed with caution; as always, more emphasis should be placed on effect sizes and confidence intervals (Nakagawa and Cuthill 2007). To visualize the effects of complex interactions, we randomly generated a new data set based on the values in our experimental data set and predicted responses across 10 varying levels of hue and saturation and six levels of luminance (fig. 3*A*). In addition, to provide a wider coverage of the avian color space, we used our final model to predict responses to an array of 1,269 Munsell color chips (Parkkinen et al. 1989; Gama and Davis 2018). Then, we interpolated a surface of predicted host responses by using a thin plate spline regression in the "raster" package (Hijmans 2016) and plotted a surface of rejection probabilities across the avian color space. All analyses were conducted in R version 3.1.2.

Table 1: Comparisons of the relative stimulation of the blackbird's four photoreceptors (quantum catches) when viewing experimental egg models versus real eggs

Photoreceptor	Bartlett's K^2	Wilcoxon rank-sum W
UVS	51.0^{***}	53,285
SWS	610.6^{***}	$43,230^{*}$
MWS	$1,873.0^{***}$	49,189
LWS	658.3^{***}	$61,934^{**}$

Note: Quantum catch is the proportion of incident photons captured by each photoreceptor. A significant difference in the Bartlett's test (K^2) demonstrates a difference in the perceived variance in color between experimental and real eggs. For each photoreceptor, the perceived color variance was greater for experimental eggs (i.e., a wider range of colors). A significant difference in the Wilcoxon rank-sum test (W) demonstrates a difference between the perceived color of experimental egg models and real eggs. UVS = ultraviolet sensitive; SWS = short-wavelength sensitive; MWS = medium-wavelength sensitive; LWS = long-wavelength sensitive.

* $P < .05$.

** $P < .01$.

*** $P < .0001$.

Results

Data from the 15 control nests supported the previous conclusions that nest desertion was not a response to parasitism in this population of blackbirds (Samas et al. 2014; Soler et al. 2015). Specifically, using the newly collected data, we found that desertion rates at experimental nests (11%, $N = 82$, i.e., 73 acceptance and rejection responses plus 9 desertions) did not statistically differ from desertion rates at control nests (0%, $N = 15$ control nests; odds ratio = 0, 95%

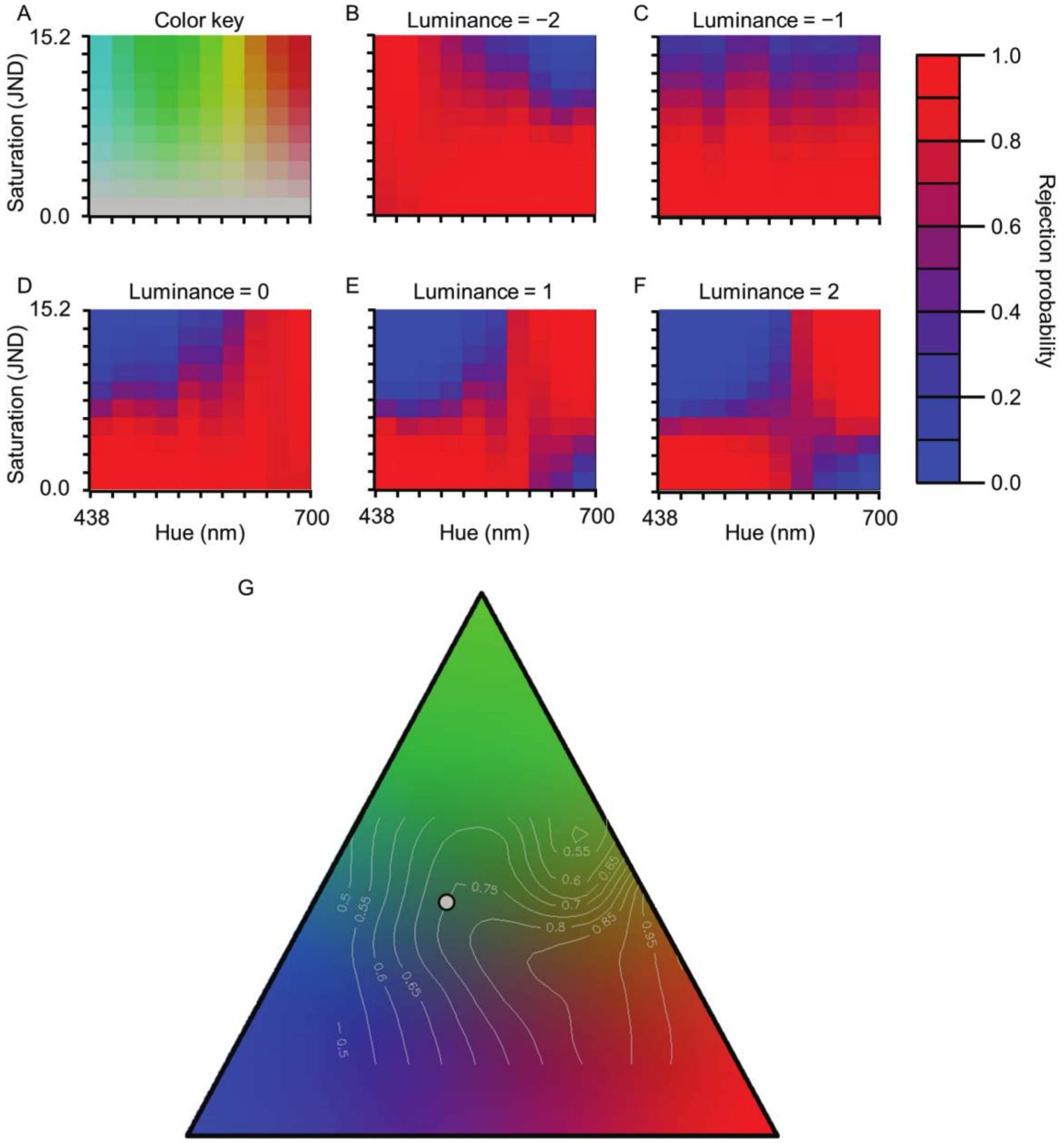

Figure 3: The predicted probability of host response (0 = accept; 1 = reject) toward colorful egg models with respect to their hue and saturation (*A*; for a color key, see the top left panel) across a range of luminance values (*B–F*; each panel represents hues and saturations of different luminance values; values are shown above each inset). Then, using this model, we predicted responses to a wide range of 1,269 Munsell color chips (*G*; Parkkinen et al. 1989; Gama and Davis 2018) and plotted the predicted host responses as contours within an avian tetrahedral color space (plotted only within the sampled range). This study was designed to examine broad patterns of host response across the avian color space based on hue, saturation, and luminance. Thus, the finely graded region of acceptance (gray dot) previously found (Hanley et al. 2017) was not detectable at this resolution. Data underlying this figure have been deposited in the Dryad Digital Repository (https://doi.org/10.5061/dryad.q293c9g; Hanley et al. 2019*a*).

CI = 0.00–3.12, $P = .35$). Therefore, nests deserted during the 6-day period ($N = 9$) were excluded from further analysis, leaving 73 responses (either acceptances or rejections) to 73 unique colors. These desertion rates were similar to those calculated by previous studies that showed that desertion rates of model eggs varied from ~6% to ~17% for blue models (“redstart” model eggs) and spotted models (“meadow pipit” model eggs), respectively (data from fig. 3 in Samas et al. 2014), as well as to the desertion rates at control nests in the same populations (~13%; data from fig. A1*b* in appendices in Samas et al. 2014). Given our results (which are consistent with previous findings), and since only nine nests were deserted in this study, we decided not to run another set of analyses considering desertions as a response (such reanalyses did not change results in previous studies; Samas et al. 2014).

Flushing at the time of experiment, laying date, nest age, clutch size, year, and quantum catch of the UVS cone did not significantly predict host response (table 2). However, the hue, saturation, and luminance of the foreign eggs predicted egg rejection behavior in blackbird females (table 2; fig. 3*B*–3*F*). There was a significant three-way interaction among these color variables. We found that, generally, egg models with shorter-wavelength hues (e.g., blue to green) were more likely to be accepted than egg models with longer-wavelength hues (e.g., oranges and reds; table 2). The exception was that when eggs were a dark saturated red-orange color, they were generally accepted; however, other dark colors were generally rejected. Generally, less saturated (less colorful) eggs were more likely to be rejected than eggs with greater saturation, except for red eggs that were particularly bright, with low saturation values (a nearly white color that would appear slightly pink). Although the rejection rate was relatively high in this study, 78% ($N = 121$ of 155 eggs from the combined data set), there was no evidence of rejection rates reaching a plateau at either the acceptance floor or the rejection ceiling (fig. 3). Contrary to our expectation, quantum catch of the UVS cone did not predict host egg rejection rates (table 2). These findings illustrate that this host is likely to reject eggs near the achromatic point of the avian visual color space and eggs that appear particularly red orange (fig. 3*G*).

Table 2: European blackbird egg rejection probabilities

	Full model		Final model	
Predictor	Logit	SE	Logit	SE
Intercept	2.06^{*}	.90	$.92^{***}$	.31
Hue	$.73^{***}$	.27	$.70^{***}$	.26
Saturation	$-.72^{*}$	.34	$-.68^{*}$	.33
Luminance	−.42	.32	−.37	.27
Hue × saturation	$.90^{*}$	.50	$.78^{*}$	.48
Hue × luminance	.59	.39	.53	.35
Saturation × luminance	.14	.48	.09	.44
Hue × saturation × luminance	$.83^{*}$	.57	$.76^{*}$	.55
UV quantum catch	−.05	.52		
Laying date	.10	.27		
Clutch size	.30	.24		
Flushed	-1.43^{+}	.88		
Nest age	.11	.30		

Note: Parameters from a generalized linear model (GLM) containing potential covariates (full model) and the parameters from a GLM reduced via sequential backward elimination of nonsignificant terms. Variance inflation factors did not exceed 2.65 for any parameter in the full or final model or in any eliminated models. Both the full ($R^2 = 0.22$, $\text{AIC}_c = 172.70$, $\chi^2 = -23.8$, $P = .05$) and final ($R^2 = 0.17$, $\text{AIC}_c = 166.17$, $\chi^2 = -18.5$, $P = .03$) models were significant (where AIC_c is the corrected Akaike information criterion). Year was nonsignificant in either model. No variance inflation factor exceeded 2.65 in the full or final model or in any eliminated models.

$^{+}$ $P < .10$.

* $P < .05$.

*** $P < .001$.

Discussion

By sampling across an unprecedented range of the avian color space, we found that blackbirds respond directly to the hue, saturation, and luminance of foreign egg models. Blackbird females accepted eggs with shorter-wavelength colors (e.g., blue and green) more often than eggs colored with longer-wavelength colors (e.g., red and orange; fig. 3*A*) when those eggs were both saturated and relatively bright. Overall, blackbirds were more likely to reject eggs that were less saturated (e.g., gray) and darker. Previous research did not find that achromatic contrast (i.e., perceived differences in luminance) predicted egg rejection responses in this species (Hanley et al. 2017). In turn, our results illustrate that eggshell luminance did significantly predict blackbird response to a wider array of egg colors (table 2). Importantly, in this study we aimed to examine perceived luminance rather than achromatic contrast between a host's own egg and the foreign egg model. Our findings suggest that hue (the type of color, e.g., blue, brown, green, or red), saturation (the intensity of that color), and luminance (the perceived brightness) inform host egg discrimination.

Although our approach to broadly sample colors across the avian visual space may mask fine-scale patterns (see fig. 3*G*) detected previously (Hanley et al. 2017, 2019*b*), it illustrates that rejection behavior can be predicted by color perception rather than perceptual distances between host and foreign eggs. In addition, our findings uncover large-scale patterns in greater specificity (e.g., how interacting color components may lead to divergent responses) than any previous study. Moreover, it illustrates the role of individual color components (hue, saturation, and luminance) on host decision-making in the wild, suggesting that the color-based host responses documented here, and previously (Hanley et al. 2017, 2019*b*), may be the product of a novel decision rule.

These color-biased responses may be due to underlying cognitive processes, as in other examples of receiver bias (Ryan 1999). For example, such host responses could be explained by categorization (Harnard 1987), where discriminable colors are treated as equivalent (e.g., a host's acceptance of a vibrant blue-green egg when their own is dull); generalization (Ghirlanda and Enquist 2003), where conditioned responses for one stimulus (e.g., a brown parasitic egg) are attributed to novel stimuli (e.g., a novel dark red egg); or both. Although determining the cognitive mechanism underlying these choices will require further study, there may be a number of advantages for hosts that base egg discrimination decisions on these components of color rather than on the perceived differences in color between their own and parasitic eggs. Decisions based on colors (rather than color comparisons) allow for template-based recognition when hosts must discriminate the eggs of multiple parasites (Bán et al. 2013); however, if this is the case, the template would be a more saturated blue green than their own eggs because blackbirds generally appear willing to accept eggs bluer than their own (fig. 3*D*–3*F*; Hanley et al. 2017, 2019*b*). Regardless of the cognitive mechanism, decisions based on color alone may allow naive hosts to use familiar color information for egg rejection decisions, rather than basing those decisions on interegg comparisons that evolve over long periods of time (Hauber and Sherman 2001).

Alternatively, these color-biased responses may be due to how the color signal is received by the host rather than how it is processed. For example, variation in light intensities can alter avian perceived hues (Wright 1976); thus, relying on multiple components of color information for egg rejection experiments may be adaptive for hosts through the degeneracy (shared message) of these color signals (Hebets et al. 2016). Moreover, birds are better able to discriminate long-wavelength colors such as brown than short-wavelength colors such as blue (Peiponen 1992); they are also more sensitive to these colors because they have more medium- and long-wave-sensitive cones (Hart et al. 2000, 2005). Last, the incident light around bird nests may vary more in certain components (e.g., green light), making the discrimination of blue-green eggs more challenging. If hosts use multiple components of color, then when one component of perceived coloration is less reliable, hosts may use another and examine eggs for longer periods of time. Indeed, previous research has found that longer periods of egg inspection result in a higher likelihood of egg rejection (Požgayová et al. 2011; but see Honza et al. 2004). We encourage future research focused on determining whether these responses are a by-product of the avian visual system or the result of a novel cognitive decision rule.

It is unclear why blackbirds did not use perceivable UV variation when discriminating eggs in this study, because UV signals have been found to be important for other hosts, including congeneric thrushes (Honza et al. 2007; Cassey et al. 2008; Honza and Polačiková 2008; Abernathy and Peer 2015; Šulc et al. 2016; but see Croston and Hauber 2014). However, previous studies either quantified UV reflectance or experimentally varied UV independently of other parts of the spectrum, whereas we used estimates of UV quantum catch. The limited UV reflectance in both host and model eggs likely explained why hosts' decisions did not appear to be related to perceived UV variation (also see Abernathy and Peer 2015). UV light contributes relatively less to solar irradiance than other wavelengths (Endler 1993), and diurnal variation in UV light is orders of magnitude greater than variation in human-visible (400–700 nm) light (Fligge et al. 2001), which potentially makes UV an unreliable signal. Although we used a standardized illuminant for our calculations, perceived variation in UV was low even when using an idealized illuminant (100% at all wavelengths), because our model eggs, just like real eggs, have relatively low UV reflectance (table 1). We recognize that some birds, particularly cavity nesters (Avilés et al. 2006), may rely on UV information (Cherry and Bennett 2001), but other wavelengths likely provide the blackbird with considerably more information; thus, it is unsurprising that they did not base their decisions on UV light.

In general, the blackbirds' rejection rates were high across all colors, which corresponds with previous studies using eggs of various colors in a variety of geographically independent populations (Davies and Brooke 1989; Moksnes et al. 1991; Polačiková and Grim 2010; Grim et al. 2011; Hauber et al. 2014; Samas et al. 2014; Soler et al. 2015). However, considering that blackbird eggs are speckled (fig. 1*A*) and the model eggs were not, this was not a surprising finding. Recent research on the American robin (*Turdus migratorius*), a related host species, has found that the chromatic contrast of spot colors to eggshell ground coloration was also a significant predictor of rejection responses (Dainson et al. 2017). Future research should explore how spots modulate these color-based rejection responses (e.g., Hanley et al. 2019*b*).

Our findings provide insights into the recognition process that hosts use for egg discrimination decisions. We quantified avian-specific color descriptors (hue, saturation, and luminance) to describe host responses and provide a detailed quantification of their responses across the avian color space. These findings show that a blackbird's rejection decision can be predicted by all three interacting components but that UV does not predict their responses. These findings should encourage future studies examining host responses across their visual spaces in a wide array of host species to determine whether these mechanisms are generalizable across wider diversity of avian taxa. Ideally, this future research should examine a range of hosts that face brood parasitism from both conspecifics (Samas et al. 2014; Lyon et al. 2015) and heterospecific parasites (Stoddard and Stevens 2011). It would be extremely useful to determine whether differing motivation levels (sensu Soler et al. 2012; Abolins-Abols and Hauber 2018), experiences over different timescales (Grim et al. 2014; Moskát et al. 2014), or avian sensory-cognitive limitations (Peiponen 1992; Manna et al. 2019) govern host biases for rejecting brown eggs. Future studies would also benefit from taking into account other sources of selection on both host and parasite egg coloration, namely, those unrelated to parasitism per se (e.g., Lahti and Ardia 2016).

The ability of organisms to accurately recognize stimuli (e.g., food, mates, and enemies) is critical for survival (Rosengarten and Nicotra 2011; Nesher et al. 2014), and assessments of perceptual distances are not the only mechanism available for discrimination tasks. We strongly encourage researchers to explore decisions across traits' entire phenotypic spaces, as the responses adaptive at one end of a phenotypic range may not be adaptive at another. This approach can help disentangle hitherto unexplored selective constraints on the evolution of parasitic eggshell coloration. In addition, such holistic consideration of a trait's phenotype can provide insights into how organisms process complex signals to make decisions regarding assessments of quality (Nordström et al. 2017; Uetz et al. 2017).

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