



The Perceptual and Cognitive Processes That Govern Egg Rejection in Hosts of Avian Brood Parasites

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Hosts of avian brood parasites are under intense selective pressure to prevent or reduce the cost of parasitism. Many have evolved refined egg discrimination abilities, which can select for eggshell mimicry in their parasite. A classic assumption underlying these coevolutionary dynamics is that host egg recognition depends on the perceivable difference between their own eggs and those of their parasite. Over the past two decades, the receptor noise-limited (RNL) model has contributed to our understanding of these coevolutionary interactions by providing researchers a method to predict a host's ability to discriminate a parasite's egg from its own. Recent research has shown that some hosts are more likely to reject brown eggs than blue eggs, regardless of the perceived differences to their own. Such responses suggest that host egg recognition may be due to perceptual or cognitive processes not currently predictable by the RNL model. In this perspective, we discuss the potential value of using the RNL model as a null model to explore alternative perceptual processes and higher-order cognitive processes that could explain *how* and *why* some hosts make seemingly counter-intuitive decisions. Further, we outline experiments that should be fruitful for determining the perceptual and cognitive processing used by hosts for egg recognition tasks.

Keywords: brood parasitism, color categorization, egg rejection, opponent channels, receptor-noise limited model

INTRODUCTION

Avian brood parasitism is an alternative reproductive strategy where one female lays her eggs in another bird's nest, imposing the costs of rearing her young on a set of foster parents (Stevens, 2013). In response, hosts often evolve egg recognition abilities as a major line of defense against parasitism, which, in turn, can select for improved eggshell mimicry in their parasite and instigate a coevolutionary arms race (Dawkins and Krebs, 1979; Davies and Brooke, 1989; Stoddard and Stevens, 2011). Such interactions have provided researchers with a tractable system to examine parasitic relationships and coevolution (Dawkins and Krebs, 1979; Davies and Brooke, 1989; Hauber et al., 2015b).

The perceptual and cognitive processes governing host egg recognition are central to understanding host decision-making and coevolutionary arms races (Dawkins and Krebs, 1979;

Davies and Brooke, 1989; Hauber et al., 2015b). Classic theory assumes that hosts can select for eggshell mimicry in the parasite by rejecting parasite eggs they perceive as dissimilar to their own (Dawkins and Krebs, 1979). Pioneering work by Stoddard and Stevens (2011) applied an avian receptor noise limited (RNL) model (Vorobyev and Osorio, 1998) to the common cuckoo, *Cuculus canorus*, and their respective hosts. They found that hosts with strong recognition abilities were parasitized by cuckoos that laid eggs with refined eggshell mimicry (as predicted by the RNL model). However, while useful for predicting discriminability between stimuli (Olsson et al., 2018; Price et al., 2019), the RNL model's original intent was to make predictions with which to compare behavioral responses and then infer color processing mechanisms (Osorio and Vorobyev, 2018). Contrary to traditional expectations (Brooke and Davies, 1988; Reeve, 1989), Hanley et al. (2017) illustrated that some hosts reject brown model eggs more than blue model eggs, even when those eggs were equally dissimilar to the hosts' own. In this experiment, model eggs were painted colors that specifically aligned with perceived variation in natural eggshell color (from blue-green to brown; Hanley et al., 2015). This finding has been meta-replicated in five hosts from three continents, each of which face distinct forms of parasitism (Abolins-Abols et al., 2019; Hanley et al., 2019b; Manna et al., 2020); however, not all hosts will accept any egg models painted "blue" (Langmore et al., 2005; Begum et al., 2012; Hanley et al., 2019a; Abernathy et al., 2021). These counter-intuitive and, at times disparate, findings raise the question, "why have these hosts deviated from our null expectations"?

Here, we explore alternative visual-cognitive processes that may explain such deviations from the expected RNL model. Specifically, we describe color vision in birds by explaining how color is both received and perceived. We then outline the discrimination challenge facing hosts and describe a higher-level cognitive process (categorization) that hosts may use to process this color information during decision-making (Harnad, 1987; Shepard, 1987; Goldstone and Hendrickson, 2009). Our goal is to contextualize previous findings of strikingly similar color-biased rejection behaviors by describing egg recognition tasks from color reception through perception (Figure 1). Finally, we provide potential experimental frameworks to aid future investigations into the perceptual and cognitive processes used by hosts for egg discrimination tasks.

Color Reception

Birds are thought to have excellent color vision (Jacobs, 1981; Goldsmith, 1990; Hart, 2001; Ödeen and Håstad, 2003). They possess four types of single-cone photoreceptors, sensitive to ultraviolet (or violet), short, medium, or long wavelength light (Hart, 2001). Avian color reception is thought to be based on the stimulation of these single cones (Hart, 2001; Ödeen and Håstad, 2003), where estimates of quantum catches (i.e., the number of photons being absorbed by the cone from the stimulus) approximate the stimulation of each photoreceptor:

$$Q_i = \int_{300}^{700} R_i(\lambda) S(\lambda) I(\lambda) O(\lambda) d\lambda$$

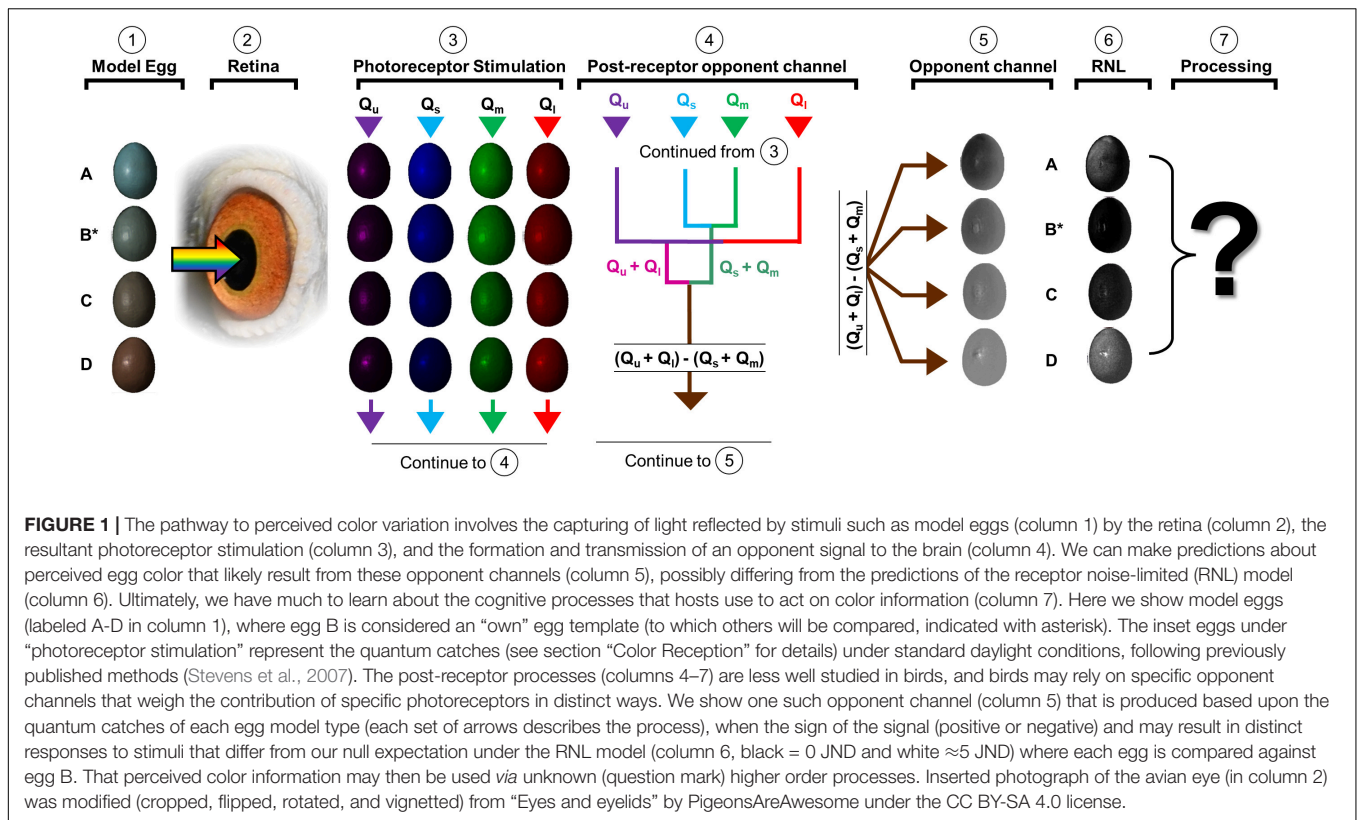
Where Q_i represents the quantum catch for receptor i , R is the sensitivity of photoreceptor i after accounting for oil droplet transmittance, S is the reflectance of a stimulus, I is the irradiance in photon flux, and O is the ocular media that narrows the sensitivity of photoreceptors in birds (Bowmaker et al., 1997; Vorobyev, 2003). By convention, we refer to the quantum catches of the ultraviolet/violet-, short-, medium-, and long-wavelength sensitive photoreceptors as Q_u , Q_s , Q_m , and Q_l , respectively.

Color Perception

Before a color can give rise to a perceptual experience in an organism, the color that is received by the eye must be transformed and transmitted to the brain (Osorio et al., 1999; Kelber, 2016; Price et al., 2019). This is done by forming opponent channels that contrast received quantum catches against each other (Figure 1), a process that underlies color discrimination in a range of organisms (Osorio et al., 1999; Ventura et al., 2001; Rocha et al., 2008; Kelber, 2016; Price et al., 2019). In theory, related opponent channels [e.g., $(Q_u+Q_l) - (Q_s+Q_m)$ and $(Q_s+Q_m) - (Q_u+Q_l)$] can produce signals that vary in sign (positive or negative) and therefore may result in two different responses. Unfortunately, the actual neural mechanisms of each channel—and, indeed, the total number of channels used—are unknown in birds (Kelber, 2016; Price and Fialko, 2018; Vasas et al., 2018; Price et al., 2019). This makes it challenging to model the actual signals reaching the avian brain.

To circumvent this difficulty, Vorobyev and Osorio (1998) developed the RNL model that predicts discriminability between stimuli. In this model, the actual opponent channels are unimportant and the sign of the signal makes no difference on model output (Vorobyev and Osorio, 1998). This model assumes that visual signals and discrimination thresholds are determined by photoreceptor noise (Vorobyev and Osorio, 1998), that there are one fewer opponent channels than photoreceptor types, and that altering light levels do not change perceived differences between stimuli (Kelber, 2016). The RNL model predicts differences between stimuli in just noticeable differences (JNDs), classifying stimuli as either discriminable (>1 JND) or not discriminable (<1 JND). Although in practice, it is generally recognized that the theoretical threshold of 1 JND is likely overly conservative in most natural contexts, and more realistic thresholds may be set ~ 2 JNDs (Spottiswoode and Stevens, 2010, 2012; Stevens et al., 2013). This model is appealing because it accurately estimates visible contrast, at least in some contexts (e.g., brightly lit conditions), provided reflectance spectra for two stimuli (e.g., those in a detection or discrimination task), spectral sensitivity estimates of each of the organism's photoreceptor types (Price et al., 2019), and the irradiance of the environment (Endler, 1993) are available.

However, there are certain conditions that may impact the RNL model's ability to accurately predict discriminability. For example, this model does not currently account for how visual contrast against the background impacts the thresholds beyond which two stimuli can be discriminated (i.e., for discrimination tasks). When viewing colorful stimuli, most animals will compensate for differences in light conditions through a process known as chromatic adaptation (Lind, 2016; Price et al., 2019).



In this process, when the background predominantly reflects long-wavelength light (typical in birds’ nests), the viewer will upregulate short-wavelength receptor signals (e.g., blue) and downregulate long-wavelength receptor signals (e.g., brown; Price et al., 2019). Consequently the predicted *detection* of blue-green eggs in brown nests is, rightly, improved (higher JND) by accounting for the nest background (Price et al., 2019). However, animals tend to perform better on *discrimination* tasks (e.g., comparing a parasite’s egg and a host’s egg) when stimuli are more similar to the background (e.g., two brown eggs on a brown nest) and poorer when stimuli are more different from the background (e.g., two blue eggs on a brown nest); thus, chromatic adaptation can effectively alter the threshold necessary to differentiate stimuli (Krauskopf and Gegenfurtner, 1992; Lind, 2016; Price et al., 2019). Currently, the RNL model does not account for these effects for discrimination tasks.

Higher-Order Processing

Most studies on color discrimination assume that animals use low-level cognitive mechanisms simply based on discrimination thresholds (Kelber and Osorio, 2010); however, previous research has provided evidence of decision-rules based on higher-level cognitive mechanisms in invertebrates, fish, mammals, and even in birds (Tapper and Halpern, 1968; Sandell et al., 1979; Nelson and Marler, 1989; Poralla and Neumeyer, 2006; Ham and Osorio, 2007; Benard and Giurfa, 2008; Avarguès-Weber et al., 2011; Lachlan and Nowicki, 2015; Renoult et al., 2015; Caves et al., 2018). One such higher-level cognitive process is

categorization, which occurs when responses to stimuli vary less within categories than between categories (Repp, 1984; Harnad, 1987; Treisman et al., 1995). This is known as a boundary effect, which is a hallmark test of categorical perception and can only be assessed measuring responses across a phenotypic range that spans both sides of a decision boundary (Harnad, 1987; ten Cate and Rowe, 2007; Kelber and Osorio, 2010; Hauber et al., 2015b). Categorization is thought to increase the speed, accuracy, and certainty of choices, while reducing the requirements for neural processing (Nelson and Marler, 1989; Kepecs et al., 2008), particularly useful for performing unfamiliar tasks or when information is uncertain (Dukas and Waser, 1994; Benard et al., 2006; Kepecs et al., 2008). Although the potential for hosts to use color categorization in egg recognition has been discussed previously (Spottiswoode and Stevens, 2010; Hanley et al., 2017), and tests have illustrated a clear decision boundary (see figures S3 and S4 from, Hanley et al., 2017), no study has yet confirmed that hosts use categorization for egg recognition (Green et al., 2020).

DISCUSSION

By providing reasonable predictions about perceivable differences between host and parasite eggs, the RNL model has proven a crucial method for testing certain hypotheses surrounding co-evolutionary arms races between host perception and parasite egg phenotypes (Spottiswoode and Stevens, 2010; Stoddard and Stevens, 2011). Comparisons between the predictions of the RNL model and actual host responses can demonstrate

higher-order processes, such as categorization (Nelson and Marler, 1989; Caves et al., 2018), or help determine the discrimination thresholds necessary for specific egg recognition tasks (Lind, 2016; Olsson et al., 2020). Such experiments would refine our understanding of the perceptual and cognitive processes that underly egg recognition decisions (e.g., opponent channels, chromatic adaptation, and categorization) and advance our understanding of host-parasite coevolutionary dynamics. Here we outline tests necessary to explore hitherto untested perceptual and cognitive processes, which may explain why some hosts' behaviors appear to deviate from the expectations of the RNL model (e.g., rejecting brown but accepting equally dissimilar blue eggs).

Host Selection for Proposed Tests

The experiments we outline below are ideally suited for hosts traditionally considered intermediate rejecters (Rothstein, 1975; Davies and Brooke, 1989; Peer and Sealy, 2004), rather than hosts that unilaterally accept or reject eggs. Additionally, these tests are suited for hosts with intermediate, rather than extreme, eggshell colors so that experimental egg model stimuli can be realistically bluer or browner than the host's. In such an experiment, a researcher would insert a single egg model, either experimental or control, into each host's nest and record their response (reject/accept) within a predefined period (Canniff et al., 2018). We advocate that researchers estimate avian-perceived coloration of each host egg (rather than average host color as in Hanley et al., 2017), experimental egg, and nest, in addition to measuring the irradiance at each nest, as these data are vital for interpreting host behavioral responses.

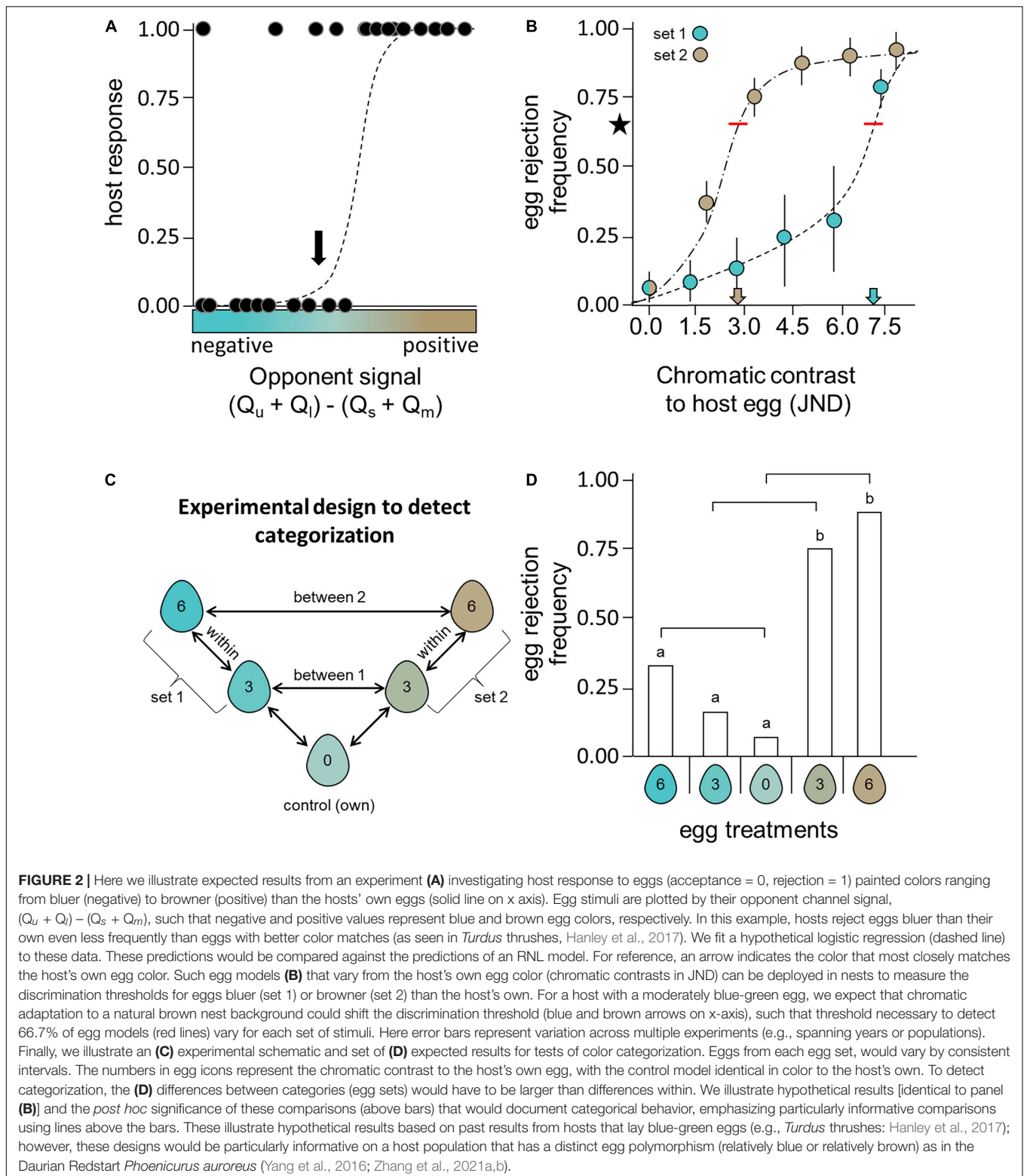
Perceptual Mechanisms

Egg rejection studies using egg models varying in coloration along a continuous range would be particularly useful for determining whether a host's response is governed by a particular opponent channel (Hanley et al., 2017, 2019b; Abolins-Abols et al., 2019; Manna et al., 2020). Such experiments (Figure 2A) would allow a researcher to determine whether host response is better predicted by opponent channel(s) or discriminable differences predicted under the RNL model and also whether responses vary sharply anywhere along that color range (decision boundary, see below). This could be a fruitful line of research, since past studies have found that individual photoreceptor quantum catches provided better predictions of host response than discriminable differences predicted under the RNL model (Cassey et al., 2008; Hauber et al., 2020). If hosts used a common opponent channel, that may explain why disproportionate rejections of brown eggs have been found in a range of hosts (Stokke et al., 2007; Cassey et al., 2008; Soler et al., 2012; Hanley et al., 2017, 2019b; Abolins-Abols et al., 2019; Manna et al., 2020). If such a common channel exists, and is used for egg recognition, it most likely broadly distinguishes short- from long-wavelength dominated colors (e.g., blue and brown, respectively). Still, while uncovering a specific shared opponent channel used by diverse hosts would be exciting, other aspects of visual perception might also explain host behaviors that deviate from our null expectations.

Chromatic adaptation to the (typically) brown nest background provides one such intriguing possibility. Lind (2016) demonstrated that the thresholds necessary for color discrimination can shift depending on the contrast between the color of the stimuli and the nest background. Thus, hosts with blue-green eggs would face a comparatively more challenging task when discriminating a blue egg (i.e., higher discrimination threshold) than discriminating a brown egg (i.e., lower discrimination threshold). Consistent with this observation, hosts found to disproportionately reject brown egg models laid (at least moderately) blue-green eggs (Honza et al., 2007; Cassey et al., 2008; Soler et al., 2012; Hanley et al., 2017, 2019b; Abolins-Abols et al., 2019; Manna et al., 2020). Although past experiments found that nest contrast did not influence host egg recognition (Aidala et al., 2015; Hauber et al., 2015a), a blue nest lining did increase performance on an egg discrimination task by 25% in the blue-green egg laying American robin *Turdus migratorius* (Aidala et al., 2015). We feel this is still a promising line of research, particularly if future studies employ an experimental manipulation of nest background (Aidala et al., 2015) alongside sufficient variation in the color of egg stimuli to determine threshold values (sensu Lind, 2016). We suggest measuring the discrimination thresholds by recording behavioral responses to sets of blue-green and brown egg stimuli sufficiently diverse to surpass threshold levels (e.g., 66.7% rejection rates; see Figure 2B) on high and low contrast nest backgrounds.

Cognitive Mechanisms

If host responses show evidence of a sharp decision boundary (Figure 2A), subsequent experiments should test for color categorization. We suggest deploying discrete sets of egg models of carefully designed colors (Nelson and Marler, 1989; Cheke et al., 2006; Ham and Osorio, 2007; Caves et al., 2018), rather than eggs with continuously varying colors (sensu Hanley et al., 2017). For example, egg sets could be bluer (set 1) and browner (set 2) than the host's own (Figure 2C), but of identical brightness. Within each set, one stimulus (stimulus 1) should be relatively similar (e.g., 3 JND) to the host's own egg (the control stimulus) and differ from the next stimulus (stimulus 2) in the set by an identical degree (e.g., 3 JND). Importantly, sets of stimuli should span the previously detected decision boundary, and there must be comparable perceivable differences within and between categories. While our focus is on colors ranging from blue-green to brown, other color ranges can be explored and more colors can be added as necessary. Color categorization would be detected if differences in host responses are significantly greater across the category boundary (see above) than within either category. Although this is a necessary follow-up test to confirm color categorization in hosts (Green et al., 2020), it may not reveal the basis for such categorical behavior. Typically, categorical behavioral responses in an experiment such as the one we propose (Figure 2) would imply hosts assign categorical labels to distinguishable egg stimuli (e.g., egg sets); however, identical responses may result from other processes (e.g., chromatic adaptation altering discrimination thresholds for certain discriminations tasks;



Figures 2B,C). Regardless of the underlying mechanism of categorical behaviors (e.g., Caves et al., 2020), such rejection behavior would select for eggshell phenotypes in novel and unappreciated ways.

Expected Evolutionary Outcomes

Importantly, these perceptual and cognitive processes (i.e., chromatic adaptation, categorization) may all impact host egg recognition, and may not be mutually exclusive. Each can be

tested by comparing host behavior to the predictions of the RNL model, and would impact host-parasite dynamics in interesting ways. For example, we would expect that heavily parasitized host populations that lay blue-green eggs would evolve even bluer eggs than unparasitized populations, under either categorization or chromatic adaptation, due to their preferential rejection of brown eggs (Soler et al., 2012; Hanley et al., 2013). In these cases, host discrimination might not only select for parasite eggshell mimicry, but also for shifts of the discrimination threshold itself (**Figure 2B**). We argue that these aspects of perception and cognition are as vital to coevolutionary arms races as the egg traits that are selected. Furthermore, we expect that the cognitive mechanisms underlying host egg recognition will be more plastic (Buchanan et al., 2008) than their egg and visual morphologies, which are, respectively, constrained and conserved traits (Ödeen and Håstad, 2003; Hanley et al., 2015). Focusing research attention on these more labile cognitive processes will likely be fruitful for determining the role hosts play in shaping coevolutionary dynamics.

Conclusion

In this perspective, we propose that hosts' discontinuous responses to continuous variation in eggshell color could be explained by more explicit perceptual (opponent channels, chromatic adaptation) and cognitive (categorization) models. By outlining fruitful directions for future research, we encourage researchers to use the RNL model as a null model with which to compare other higher-level processes. Avian brood parasitism provides an ideal system to not only learn about parasitism and coevolution (Soler and Soler, 2000; Stoddard and Hauber, 2017), but also the hitherto unidentified perceptual and cognitive

mechanisms (Stoddard and Hauber, 2017) used by wild birds. By developing experiments explicitly designed to discern the underpinnings of avian vision, we can learn more about how birds interpret the world around them, an understanding that is vital to grasping their past, present, and future evolutionary trajectories (Endler and Mielke, 2005; Endler et al., 2005; Stevens, 2011), as well as to informing current conservation efforts (Blackwell et al., 2012; Dominoni et al., 2020). It is our hope that this manuscript will catalyze future investigations into the cognitive processes that underly perception and decision-making in broad taxonomic groups and contexts.

DATA AVAILABILITY STATEMENT

The original contributions presented in the perspective contain no data, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

DH provided the concept. DH, SR, and JV proposed experimental designs. All authors worked to develop and revise the writing.

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