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Intraspecific Signaling as an Adaptive Force in the Evolution of Blue-Green Eggs in Robins: A Review of Recent Work

ABSTRACT

Previous theories have been unable to explain the vivid blue-green coloration found in the eggs of robins or other passerines, which seems to be selectively neutral or maladaptive for cryptic or egg-recognition purposes. A recent body of work has examined a new hypothesis, which suggests that blue-green egg color is a sexually selected signal indicating clutch quality and prompting higher male investment, as the pigment responsible for the blue-green color is costly for females to deposit in eggshells. Links between egg color intensity and female or egg quality have been well supported in a number of passerine species. Effects of this correlation on male behavior have been less consistently shown across species, although evidence exists for male response to egg color in American robins (*Turdus migratorius*). This topic is of importance to the understanding of sexually selected “honest” or “dishonest” signals of quality, which are well-documented in physiological characteristics of individuals but less understood when they occur in eggs or offspring.

INTRODUCTION

The bright blue-green coloration of robin eggs has been a persistent enigma in ornithology since Wallace (1889) suggested that the main adaptive function of egg coloration was to conceal eggs from predators in the nest's particular microenvironment. A number of possible adaptive explanations for the bright coloration will be discussed in this review, with a focus on evaluating the evidence supporting the theory that the pigmentation functions as a sexually selected signaling mechanism to indicate female and clutch quality to males.

Eggs were likely ancestrally white (Wallace 1889) until selective pressure emerged for pigmentation and patterning in the shells as a result of diversification in nesting sites and behaviors. Immaculate white eggs are mainly preserved in hole-nesting species where there is less pressure for crypsis in eggs to avoid predation (Kilner 2006). Coloration in other songbird eggs is mainly produced by one or both of two pigment compounds: biliverdin (blue-green) and protoporphyrin (brown). Biliverdin is present in the bodies of adults in good condition as a powerful antioxidant that protects against peroxyl and hydroxyl free radicals (Moreno 2003). Protoporphyrin, a metabolite intermediate in the production of heme, is associated with stress in individuals when found in the liver, but the relationship between eggshell deposition and female body condition is unknown (Moreno 2003).

ADAPTIVE PRESSURES ON COLORATION

In their comprehensive review of adaptive forces acting on eggshell coloration, Underwood and Sealy (2002) suggested that egg coloration mainly resulted from two selective pressures: predation avoidance and egg-recognition.

Blue color in eggs does seem to serve a camouflage purpose in some Amazonian species, where bluer eggs are found in nesting sites in green foliage and direct sunlight (Oniki, 1979, 1985). Selection for cryptic egg coloration, however, has not been supported in passerines that build large, conspicuous nests off the ground. Götmark (1992) filled artificial song thrush

(*Turdus philomelus*) nests with white-painted, blue-painted, or cryptically-spotted eggs. No significant difference in predation rates was found between the nests, suggesting that blue-green pigmentation was a neutral trait with regard to selection. When similar artificial eggs were placed in trees without nests, a slightly higher survival rate was seen among cryptically-spotted eggs than among either white or blue eggs. Götmark suggested that predators were likely to locate conspicuous nests before the eggs, resulting in the even predation rates across egg colors when inside nests. Weidinger (2008) corroborated this hypothesis by substituting real eggs of different colors into artificial nests, again finding no significant difference in predation rates.

The use of artificial nests in experiments dependent upon nest appearance raises doubts as to the findings because of the extreme difficulty in imitating the appearance, structure, and placement of natural nests. Westmoreland (2008) bypassed this risk by the sequential substitution of clutches of differently-colored eggs into preexisting, natural robin nests, to control for the effects of nest size, location, and appearance on clutch survival. Little difference was found in overall survival between egg colors, although red-winged blackbird eggs (light blue with brown markings) were discovered by predators earlier than eggs of brewer's blackbirds (blue or brown with brown speckles) or yellow-headed blackbirds (tan with brown markings). Overall, no evidence exists for a cryptic benefit of blue-green eggs in robin nests; indeed, studies indicate that the coloration is either selectively neutral or maladaptive.

Underwood and Sealy (2002) also suggested a role for pigmentation in egg recognition, allowing individuals to distinguish their own eggs from those of other conspecifics as well as brood parasites. This hypothesis is salient, as robins are one of few species known to eject parasitic cuckoo eggs from their nests upon discovery (Lorenzana & Sealy 2002). Kilner (2006) suggested a co-evolutionary arms race at play between host species and their parasites, wherein parasite eggs evolve a closer mimicry of host species eggs even as host species adapt to express egg colors and patterns more difficult to imitate. However, parasite ejection rates were not found to vary significantly when robins were presented with white cuckoo eggs as opposed to blue cuckoo eggs (Lorenzana & Sealy 2002). Furthermore, 80% of robins accepted white eggs experimentally placed in their nests and 94% accepted blue eggs (Lorenzana & Sealy 2002), indicating that, even in cases of such a dramatic color difference, egg recognition is only dependent on color to a limited degree. Using avian perceptual modelling combined with eggshell reflectance data to approximate birds' perception of egg color, Croston and Hauber (2014) found that egg ejection rates are partially predicted by overall eggshell color differences; however, robins eject eggs more frequently than is predicted by perceptual color modeling alone. Together, these findings suggest that parasitism avoidance is unlikely to be the driving selective force in evolution of costly pigment expression.

Other selective hypotheses proposed to explain pigmentation have included protection from solar radiation, reinforcing eggshell strength when protein is lacking in the environment, and aposematism (Underwood & Sealy 2002). None of these hypotheses have been convincingly supported as explanations for high levels of biliverdin in robin shells. At the time when Underwood and Sealy published their review of adaptive forces acting on eggshell pigmentation, they concluded that "the adaptive significance of blue eggs remains a mystery."

A SIGNALING HYPOTHESIS

Moreno (2003) proposed a novel hypothesis to account for bright coloration, based on Zahavi's 1975 handicap theory stating that honest signs of quality in an individual must be costly to express. Because the deposition of biliverdin, a strong antioxidant, is likely to be costly to females (and females would therefore have to overcome the "handicap" of its loss to eggshells), Moreno suggested that egg coloration may have evolved as an indicator of female quality. Moreno also hypothesized that, because egg color may be capable of indicating genetic quality of the offspring in a way that egg or clutch size is unable to, males would invest more energy in clutches of brighter blue eggs based on an expectation of higher-quality offspring. This proposed signaling pathway can be divided into two phases: the honesty of signaling (*i.e.* is biliverdin content in eggs a consistent indicator of higher female quality?) and the efficacy of signaling (*i.e.* does biliverdin content in eggs influence male behavior?).

Does biliverdin content correspond to female quality or investment?

A large body of work exists in pied flycatchers (*Ficedula hypoleuca*) suggesting a close relationship between biliverdin deposition and maternal investment in the egg. The intensity of blue-green coloration in eggs has been positively correlated with female condition, maternal antibodies in the yolk, and ultimately, fledgling success (Morales *et al* 2006). Blue-green spectrographic measurements were independently linked to actual biliverdin content in the shell (Moreno *et al* 2006a). Blue-green color was also correlated with plasma antioxidant levels in females (Morales *et al* 2008), supporting the idea that higher-quality females may be in better condition to weather the antioxidant drain caused by biliverdin deposition in eggshells. Shorter wavelengths (darker colors) in reflectance measurements have also been associated with female immunocompetence and condition (Moreno 2005). Flycatchers experimentally provided with supplemental food during laying also produced heavier and brighter blue-green eggs (Moreno, *et al* 2006a)

More specific links have been found between maternal investment in the egg itself and egg color in spotless starlings (*Sturnus unicolor*). Navarro *et al* (2011) found that blue-green coloration varied with concentration and the amount of carotenoids and vitamin E found in egg yolks; eggshell color and yolk androgen concentration also varied positively with color intensity (Lopez-Rull *et al* 2009). Removal of some feathers from female starlings to experimentally deteriorate their condition resulted in a decrease in coloration intensity (Soler *et al* 2008). Although Lopez-Rull *et al* (2009) reported a strong correlation between biliverdin content and egg colorimetry, they failed to find that color intensity yielded the same predictive ability of female and egg quality that measured biliverdin content itself yielded. This disconnect raises doubts as to whether egg coloration is an accurate indicator of shell biliverdin content, a necessary intermediate step in an honest signaling pathway.

In two species of true thrushes, *Turdus merula* and *Turdus philomelos,* Cassey *et al* (2012) found that reflectance-based color measurements were poor indicators of tested shell pigment concentrations. Moreover, when avian perception models were applied to eggshell coloration, avian-perceived coloration was not consistently correlated with measures of maternal investment (Cassey *et al* 2008). These two findings raise important questions about the relationship between biliverdin content and reflectance measurements, which are generally used as a proxy for pigment concentration.

Does eggshell coloration alter male investment?

A smaller body of work has been done to test the second element of Moreno's proposed signaling pathway, theorizing that egg coloration impacts paternal investment in the clutch. Some authors have used avian perceptual modelling to cast doubt upon passerines' abilities to distinguish variation in background coloration of conspecific eggs (Cassey *et al* 2009). However, significant results in some studies linking egg colorimetry to male investment appears to eliminate this doubt.

The proposed signaling pathway is by no means universal in songbirds; no correlation was found between egg coloration and female quality or male investment in great reed warblers (*Acrocephalus arundinaceus*). It is worth noting that great reed warbler eggs exhibit substantial brown spotting, unlike those of other species discussed here, which are mainly immaculate and blue-green. However, even within species where a link has been established between female or egg quality and egg coloration, signaling does not always seem to take place. Collared flycatchers (*Ficedula albicollus*) show a clear positive correlation between female quality and intensity of blue-green pigmentation, but a clutch-substitution (cross-fostering) experiment failed to link egg color to a significant increase in either nestling feeding frequency or nest defense by the male (Krist & Grim 2007).

Other species demonstrate strong evidence of this signaling pathway. A cross-fostering study by Moreno and colleagues (Moreno *et al* 2006b) in pied flycatchers linked higher peak values of green-blue reflectance measurements in eggs to increased male provisioning on day 4 of the clutch, which in turn had a positive effect on female fitness. In a separate study, Moreno *et al* (2004) found that differences in egg coloration explained over 20% of the variation in male parental effort. Male provisioning rates were positively correlated with nestling condition.

In American robins (*Turdus migratorius*), a recent study substituted natural clutches with clutches of either unusually pale or vividly colored robin eggs and measured parental investment when the nestlings were 3, 6, and 9 days old (English & Montgomerie 2011). Male investment was significantly higher at day 3 in the vivid egg group than in either the pale or the control groups. This trend was not seen later in hatchling development. Observations of unmanipulated clutches yielded only a weak, nonsignificant correlation (weight = 0.33) between male investment and color intensity at day 3.

DISCUSSION & CONCLUSIONS

In passerine species laying immaculate blue-green eggs, the bulk of the evidence supports a significant correlation between egg quality and biliverdin concentration. As posited by Moreno's 2003 theory, this suggests biliverdin levels have the potential to be honest signals to males indicating female or clutch quality, designed to increase male investment in high-quality clutches. Male responses to this signal are not found in all species where the color-quality trend is observed. However, male behavioral responses have been observed in large-scale studies in pied flycatchers and robins, which indicate the existence of a functional signaling pathway in some species. Overall, sexual selection for signaling has been fairly well-supported in recent years as an adaptive explanation for the bright blue-green coloration.

An adaptive explanation for coloration in species where eggshell biliverdin content is not correlated with male investment (*i.e.* Krist & Grim 2007) requires more examination. The emergence of adaptively "lying" through this signaling pathway—using other pigments in the shell to mimic the visual effect of increased biliverdin—could eliminate the signaling pathway while maintaining biliverdin-rich eggs as an evolutionary artifact. Alternatively, it is possible that signaling is still present, but male responses are expressed in ways not measured by investment in the nest—for instance, increased guarding of the female to ensure paternity.

As demonstrated by Cassey *et al* (2008, 2012), the links between eggshell reflectance readings and actual biliverdin concentration also require clarification. Results obtained using shell reflectance measurements alone should be revisited in species where the reflectance-biliverdin concentration link has been called into question. In systems where reflectance is found to be indicative of biliverdin concentration, a better understanding of how reflectance (and therefore biliverdin levels) relates to avian visual perception is needed. If both of these relationships can be positively confirmed but no male response to the signaling is detected, then it would be possible to eliminate a broken or dishonest signaling pathway and focus research on other adaptive explanations for color intensity.

A final disconnect not addressed in work done to this point involves the relationship between baseline female quality, current condition, and relative investment in eggs. Studies such as Morales *et al* 2006 assume an absolute metric of egg quality irrespective of female quality. However, phenotypic signals of female quality may be integrated with egg color to create a composite signal of clutch quality. Clutches of similar color intensity may still vary in quality depending on the baseline condition of the laying females (*i.e.* a genetically low-quality female making a large physiological investment may still produce lower-quality offspring than a genetically high-quality female making an average physiological investment in the clutch).

The findings of work in this field have advanced understanding of sexually selected signaling traits outside of the appearance or behavior of an individual. However, like most physiologically-derived signals, it depends upon varying conditions in such a way that the specifics of the signal mechanism are unlikely to be constant across different environments and species.

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I affirm that I have adhered to the Oberlin Honor Code on this assignment.

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