

Lynn Siefferman · Kristen J. Navara · Geoffrey E. Hill

Egg coloration is correlated with female condition in eastern bluebirds (*Sialia sialis*)

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Abstract Egg coloration has been hypothesized to reflect female condition. Because of the proposed physiological costs associated with deposition of biliverdin pigments and because of their conspicuousness, eggs with blue-green coloration may reliably convey information about female or brood quality. We tested the hypothesis that expression of blue-green coloration of eastern bluebird (*Sialia sialis*) eggs positively correlates to female condition. First, we documented the incidence of egg color polymorphism within the population. We observed that 98% of females laid blue-green eggs while less than 2% laid white eggs and less than 1% laid pink eggs. In a subset of clutches, we used full spectrum reflectance spectrometry (300–700 nm) to compare eggshell coloration to measures of female condition. We found that the color of eggs within clutches was more similar than the color of eggs from different clutches, and that the blue-green eggs have spectral peaks that are consistent with the characteristic absorbance spectra of biliverdin pigmentation. Females in better body condition and older females laid more colorful eggs. Moreover, individual females laid more colorful eggs later in the laying sequence. Overall, these data indicate that egg coloration covaries with female condition, suggesting that egg coloration could function as a reliable signal of female quality or that egg coloration may allow females to recognize eggs laid by conspecific brood parasites.

Keywords Egg coloration · Biliverdin pigmentation · Female condition · Age

Introduction

Many hypotheses, including camouflage and mimicry, have been developed to explain the evolutionary significance of egg coloration (reviewed in Underwood and Sealy 2002). Experimental manipulations of blue and blue-green eggs, however, have found no support for the hypothesis that such eggs are cryptic (Götmark 1992; Weidinger 2001; Underwood and Sealy 2002). Moreover, these eggs appear to be conspicuous and they are commonly laid by species that are not brood parasites. Recently, Moreno and Osorno (2003) proposed that in species with biparental care of the young, blue-green egg coloration may function as a trait that advertises the condition or genetic worth of females to males. Females could also uniquely color eggs to improve discrimination of their own eggs from those laid by a brood parasite (Underwood and Sealy 2002).

Blue-green eggs are colored by the pigment biliverdin (Kennedy and Veevers 1976) that is deposited on the shell by the mother's shell gland (Baird et al. 1975). Biliverdin is a porphyrin that results from oxidative degradation of heme (Lemberg and Legge 1949; Otterbein et al. 2003). Although bile pigments were traditionally viewed only as waste products of heme catabolism, recent research has shown that biliverdin and its reduction product, bilirubin, are potent antioxidants (Stocker et al. 1987). Biliverdin and bilirubin were also shown to be effective modulators of cell-signaling pathways (Phelan et al. 1998), and essential components in early embryogenesis (Falchuk et al. 2002). Diverting these chemicals for use in coloring eggs may be costly for females, particularly during the egg-laying period when high levels of circulating progesterone can induce oxidative stress (von Schantz et al. 1999). In zebra finches (*Taeniopygia guttata*), male and female reproductive effort decreases antioxidant defenses, suggesting that oxidative stress represents a cost of reproduction (Alonso-Alvarez et al. 2004).

The deposition of biliverdin in eggshells could signal antioxidant and anti-nitrosative capacities; thus, blue-green egg coloration could reflect female condition during the laying period. Moreover, this relationship may be reinforced if there is a trade off between the use of biliverdin for

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L. Siefferman (✉) · K. J. Navara · G. E. Hill
Department of Biological Sciences
331 Funchess Hall,
Auburn University,
Auburn, AL 36849, USA
e-mail: siefflm@auburn.edu
Tel.: +1-334-8444829
Fax: +1-334-8449234

physiological function and use of the pigments to color eggs (Moreno and Osorno 2003). Condition-dependent egg coloration could also facilitate discrimination of eggs from those laid by a brood parasite (Davies and Brooke 1988; Møller and Petrie 1991), particularly if lower condition females are more likely to parasitize the nests of high condition females. If egg coloration resulting from biliverdin and bilirubin is an honest signal of female condition, one would predict that egg coloration would be correlated with female age, body condition, and the position of egg in the laying sequence (Miksik et al. 1994, 1996; Moreno and Osorno 2003). The purpose of our study was to test the hypothesis that egg coloration is related to female condition in eastern bluebirds (*Sialia sialis*).

Eastern bluebirds are socially monogamous passerines in which females incubate eggs, males feed females during the pairing and incubation stages, and both sexes care for the young (Gowaty and Plissner 1998). The eastern bluebird is an excellent species for a study of egg coloration because they lay blue-green eggs that are likely colored by the pigment biliverdin (see spectral data in Results section). Bluebird eggs vary substantially in blue-green coloration between clutches laid by different females. In addition to typical variation in blue-green coloration of eggs, whole clutches of bluebird eggs are sometimes white or pink (Gowaty and Plissner 1998). Because bluebirds are obligate secondary cavity nesters, both males and females compete vigorously against same-sex conspecifics for nest sites (Gowaty and Wagner 1988), and conspecific brood parasitism occurs (Gowaty and Karlin 1984). Past research has demonstrated that older females and females in better body condition begin nesting earlier in the season and experience greater reproductive success (Siefferman and Hill 2005). If egg coloration is related to female condition and age, then coloration should be more similar among eggs within a clutch than among eggs in different clutches. Consequently, older females and females in better body condition should produce more colorful eggs. Moreover, if pigment deposition represents a resource investment, then egg pigmentation should covary with egg size within individual females.

Methods

We studied a marked population of eastern bluebirds on a 4-km² study site from March to August 1999–2003 in Lee County, Alabama, USA (32°35'N, 82°28'W). Nest boxes were checked daily throughout the breeding season to document the date at which the first egg was laid. We estimated the age of all newly banded birds upon capture, as either yearling (in their first year of life) or in the second or subsequent year based on the shape of the tenth primary feather (Pitts 1985). Thus, we knew the exact age of a subset of birds that were banded as nestlings on our field site. We have studied eastern bluebirds at this study site for 6 years and have found this method to be accurate compared to known-age birds.

We used both the residuals of a regression of body mass on tarsus length (Jakob et al. 1996) and the ratio of body

mass to tarsus length as indices of body condition. The results were very similar for the residual analyses and the ratio analyses, so we show only the results of the residuals of body mass on tarsus length. Body condition indices are thought to reflect variation in the quality of organisms such as health, nutritional status, and fat content (Brown 1996). Because the amount of body fat carried by individuals can change substantially with season and across a nesting cycle, body condition indices must be used with caution (reviewed in Hayes and Shonkwiler 2001). For this study, our condition index appears to be a relevant measure of individual quality. We weighed and measured all individuals in early spring during the first week of incubation, so we standardized all measures for season and point in the nesting cycle. Prior research with female bluebirds in our population showed that this measure of body condition is associated with fitness traits such as first egg date and provisioning rates to offspring (Siefferman and Hill 2005).

From 1999 to 2003, we visually classified clutches of eggs as blue-green, white, or pink. In 2003, eggs were collected for a study of yolk–hormone content (KJ Navara, unpublished data). We measured the mass of each egg to the nearest 0.001 g. We measured 106 eggs from 39 clutches laid by different females. We typically collected eggs 1, 3, 5 in the laying sequence from each clutch, but occasionally we collected eggs 2 and 4.

Reflectance was quantified with a spectrometer (range: 300–700 nm; S2000, Ocean Optics, FL), a deuterium–tungsten–halogen lamp, and a fiber-optic probe. The measurements illuminated a region 2 mm in diameter and were taken at a 90° angle to the eggshell surface. We measured the reflectance from 10×10 mm pieces of eggshell placed on matte black cardboard in a dark room. Each reading was constructed from an average of 20 reflectance curves. We took three readings from each egg, moving the probe by at least 5 mm before taking each new reading. Blue-green chroma was calculated as the proportion of the total reflectance that is in the blue-green region ($R_{400-575}/R_{300-700}$) of the spectrum. We used blue-green chroma to describe egg reflectance data because this region corresponds to the region of least absorbance (and therefore greatest reflectance) of biliverdin (Falchuk et al. 2002) and because bluebird eggs reflect light maximally in this region (Fig. 1).

We tested for normality using Shapiro–Wilk tests, and used parametric tests when data were normally distributed and nonparametric tests when assumptions of normality were violated. We used SPSS (version 11.5 Chicago, IL) software to analyze the data and all statistical tests were two-tailed. Sample sizes vary because we did not estimate the body condition and age of all females. Additionally, the white-egg clutch was excluded from some analyses.

Results

Eastern bluebirds in our population laid eggs of three morphs: blue-green, white, and pink. There was a discrete difference in spectral shape between “blue-green”, “white” and “pink” eggshells. Typical blue-green eastern bluebird

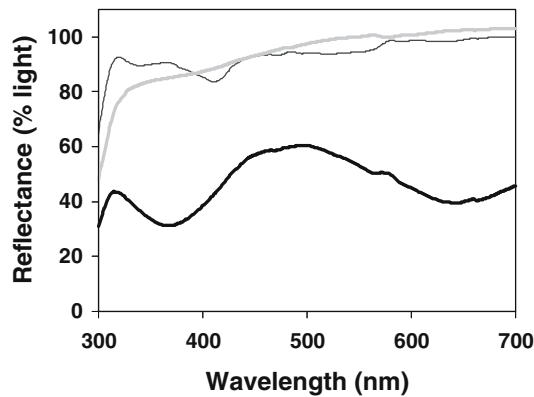


Fig. 1 Typical reflectance spectrum of a blue-green egg (thick black line), a white egg (thin black line), and a pink egg (thick grey line). Blue-green chroma is the proportion of the total reflectance that is in the blue-green region ($R_{400-575}/R_{300-700}$) of the spectrum

eggs showed two peaks of spectral reflectance. The greatest spectral peak occurred near 495 nm and corresponded to the blue-green coloration apparent to humans, while a secondary reflectance peak occurred near 320 nm, in the ultraviolet region of the spectrum (Fig. 1). The characteristic absorption profile of biliverdin based on chromatographs has two distinctive peaks at 375 and 665 nm (Falchuk et al. 2002). This is consistent with the spectral profiles of bluebird eggs (Fig. 1; note that absorbance and reflectance are inversely related). Eggs from the white clutch reflected light more consistently over the entire UV-visible spectrum (Fig. 1), suggesting that these eggs had very little or no biliverdin pigmentation. Pink eggs (collected in 2004) reflected light over the entire UV-visible spectrum; however, the longer wavelengths reflected more light than the shorter wavelengths (Fig. 1).

For five breeding seasons, we monitored 281 individual females that laid 778 clutches. Of those clutches, 767 clutches were blue-green, nine clutches were white, and three clutches were pink. Color polymorphism was consistent within clutches; if a female laid one white (or pink) egg, every egg in her clutch was white (or pink). Likewise, egg coloration was consistent among successive clutches; females that laid white (or pink) eggs in the first clutch also laid white (or pink) eggs in the second clutch. In total, 275 females (97.86%) laid blue-green eggs, five females (1.78%) laid white eggs, and one female (0.36%) laid pink eggs. Although 45% of females in our population bred in more than 1 year, none of the females that laid white or pink clutches bred in more than 1 year. We were unable, therefore, to investigate the consistency of egg color polymorphism in successive years.

In 2003, we measured the reflectance of 106 eggs from 39 nests laid by different females. One clutch measured in 2003 had four white eggs and there were no nests of pink eggs. The mean mass of these white eggs was greater than the mean egg mass of any other clutch (range in mean mass of blue-green clutches: 2.38–3.34 g vs. mean mass of white clutch: 3.44 g). Among the blue-green clutches, however, we found no significant relationship between mean egg

mass and mean egg coloration (blue-green chroma; Pearson correlation, $r=0.07$, $n=36$, $P=0.69$).

Using analysis of covariance with nest of origin as the fixed factor and number of eggs measured per clutch as the covariate, we found a significant effect of nest of origin on egg coloration (ANOVA, $F_{38,105}=5.42$, $P<0.001$) and egg mass (ANOVA, $F_{36,102}=12.24$, $P<0.001$), indicating that individual females laid eggs that differed from the eggs of other females in both color and mass.

We used paired t tests of earlier and later laid eggs to determine if there was an increase in egg mass and blue-green chroma among them. We did not necessarily collect all eggs from all nests; thus, we had an incomplete data set for laying order. For this analysis, we randomly chose one egg from either the first or the second position in the sequence to represent ‘early’ eggs, and one egg from either the fourth or the fifth position in the sequence to represent the ‘later’ eggs. We found that the eggs laid later in the laying sequence expressed significantly higher blue-green chroma (mean $\pm$ SD, $0.51\pm 3.0\times 10^{-3}$ vs. $0.49\pm 3.0\times 10^{-3}$; Student’s t test, $t=2.9$, $n=34$, $P<0.01$), and were heavier (2.94 ± 0.05 g vs. 2.86 ± 0.05 g; $t=2.4$, $n=33$, $P<0.05$) than eggs laid earlier in the laying sequence.

Using the clutch initiation date and mean coloration of each blue-green clutch, we found no significant relationship between laying date and eggshell coloration (Spearman rank correlation, $r_s=-0.25$, $n=38$, $P=0.14$). Females, however, laid significantly larger eggs later in the season (Spearman rank correlation, $r_s=0.41$, $n=37$, $P=0.01$). The white-egg clutch was laid within a few days of the mean clutch initiation date.

Using the index of female body condition and mean coloration of each blue-green clutch, we found that females in better body condition laid clutches of eggs that expressed significantly higher blue-green chroma (Fig. 2) and heavier eggs (Pearson correlation, $r=0.37$, $n=30$, $P=0.04$). Because very few individuals were fourth-year or older, we combined the data for all after-second-year females. However, we recognize that this is a rough estimate of age. Older (after-second-year) females laid significantly more pigmented eggs than younger (second year) females (Fig. 3). There was no difference, however, in the average egg mass

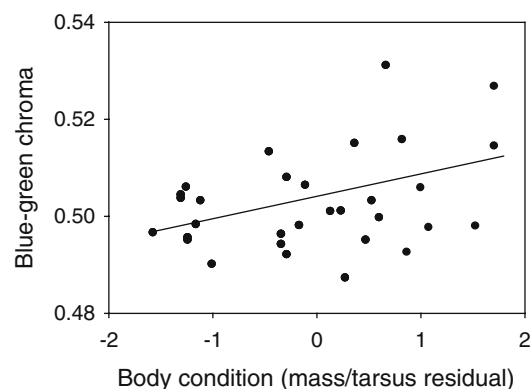


Fig. 2 Relationship between blue-green chroma of eggs and female body condition (residuals of regression of mass on tarsus; $r=0.37$, $n=31$, $P=0.04$)

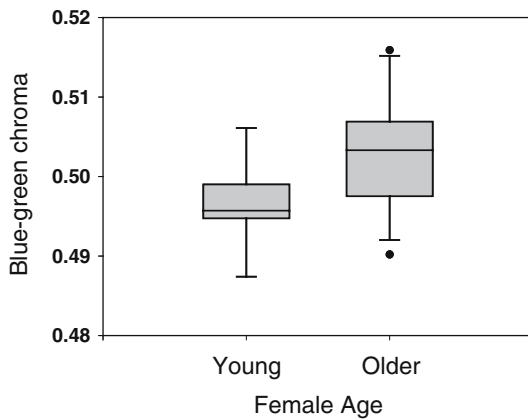


Fig. 3 Box-plots of blue-green chroma of eggs that were laid by young versus older female eastern bluebirds. Older females laid eggs that displayed a greater proportion of reflectance in blue-green wavelengths than young females ($t=2.2$, $n=9,18$, $P=0.04$). The line within each box represents the median color score. The upper and lower borders of each box are the 25th to 75th percentiles, and the lower and upper bars are the 10th and 90th percentiles

laid by second-year and after-second-year females (Student's t test, $t=-1.4$, $n=10,18$, $P=0.17$).

Discussion

Consistent with the hypothesis that biliverdin pigmentation in eggshells reflects female condition, we found that older females and females in better body condition laid the most colorful eggs. These results represent an interesting contrast to Moreno et al. (2005) in which egg coloration of pied flycatchers (*Ficedula hypoleuca*) decreased in the oldest age class, suggesting that senescing females lay less colorful eggs. Unfortunately, our rough age estimates do not allow us to properly test for an influence of senescence on egg coloration. Although the cost of depositing biliverdin pigments into eggshells is not yet understood, our observations, and those of Moreno et al. (2005), who found that egg coloration correlates to cell-mediated immunity in females, represent some of the first empirical evidence that biliverdin pigmentation is correlated with female condition. Condition-dependent egg coloration may be adaptive if males use egg coloration to make strategic decisions concerning paternal investment (Moreno and Osorno 2003), or if females use egg coloration to discriminate between their eggs and those laid by a conspecific brood parasite. A nonadaptive alternative explanation is that older bluebird females and females in better body condition may produce more biliverdin that ends up in eggshells, but the coloration of eggs has no signaling value.

There is accumulating evidence for a protective role of biliverdin / bilirubin in organism health. Biliverdin / bilirubin are antioxidants that can scavenge free radicals (Stocker et al. 1987) and can prevent pathological processes in mammals including myocardial ischemia (Clark et al. 2000), pulmonary fibrosis (Wang et al. 2002), and hypertension (Polte et al. 2002). Although this research has been con-

ducted exclusively with mammals, biliverdin / bilirubin may serve to prevent pathological processes in birds as well. The relationship between female condition and egg coloration suggests that females may be limited in the amount of biliverdin that they deposit into eggshells and that they may divert biliverdin from its role in protecting cells from injury.

Not all female bluebirds in our population produced blue-green eggs. Approximately 2% of females laid white or pink eggs that probably lacked biliverdin pigments. Because egg color morphs were consistent within females (within clutches and among successive clutches), it is likely that white and pink eggs are the result of a genetic mutation that disrupts the conversion of porphyrin to biliverdin or that prevents biliverdin deposition at the site of the shell gland. Our data are consistent with eggshell polymorphisms in the crow tit (*Paradoxornis webbiana*) in which individual females consistently lay either blue or white morphs (Kim et al. 1995).

The spectra of the blue-green eggs exhibit dual peaks: a large peak in the blue-green region of the spectrum and a smaller peak in the UV region. These spectral curves are similar to those of the pied flycatcher (Moreno et al. 2005). Two lines of evidence suggest that the UV-reflection peak of blue-green eggs is colored by the underlying eggshell (i.e., calcium) and not by biliverdin pigments. First, the white and pink eggshells also reflected light in the UV region (Fig. 1). Second, biliverdin pigments absorb relatively small amounts of UV light (Falchuk et al. 2002). Moreover, the UV-reflection peak of blue-green eggs may not have an important signaling function because avian vision is limited to wavelengths between 320 and 700 nm (Hart 2001).

Although we found that both egg mass and egg coloration covary positively with female condition, they appear to covary independently, suggesting that both egg coloration and mass reflect female quality. Prior research also suggests a link between overall egg investment and biliverdin deposition, in both pied flycatchers (Moreno et al. 2004) and house finches (*Carpodacus mexicanus*; Siefferman et al., unpublished). Females that lay darker pigmented eggs also lay larger eggs. A large body of literature suggests that larger egg size confers fitness benefits to offspring (reviewed in Williams 1994). Indeed, in eastern bluebirds, egg size influences offspring growth independent of parental quality (Robinson 2005). In eastern bluebirds, older females and females in better body condition both experience greater reproductive success (Siefferman and Hill 2005) and produce more pigmented eggs, suggesting a link between overall reproductive investment and biliverdin deposition.

Although Moreno et al. (2005) found that pied flycatcher eggs decrease in coloration with laying order, we found that both egg coloration and egg size increase with position in the laying sequence. Larger eggs in later positions in the laying sequence have been observed in several species of birds and are thought to function as a strategy to facilitate the survival of the nestlings hatched from eggs laid later in the sequence (reviewed in Slagsvold et al. 1984). This study is the first to report that eggs laid later in the sequence have

more intense egg coloration and such increase may function like increased egg size to facilitate survival of the nestlings hatched from those eggs. Parents could recognize the position of eggs in the laying sequence by assessing coloration and adjust parental care accordingly. Alternatively, increased pigmentation may simply be a by-product of the maternal strategy of allocating more resources to egg production later in the laying sequence.

A highly conspicuous trait suggests that it has a signaling function (Schluter and Price 1993). The conspicuousness of an egg is influenced by its pigmentation, the light environment in which it rests, the background, and the perceptual abilities of the receiver (Endler 1990). There may be high achromatic and chromatic contrast between the coloration of bluebird eggs and the coloration of the background nest material (based on the reflectance spectra of the nests of other bird species; Hunt et al. 2003), suggesting that bluebird eggs are probably highly conspicuous. The amount of ambient light inside the cavities of cavity-nesting species (*Parus major*, *Ficedula hypoleuca*, *Passer domesticus*), however, is relatively low (Hunt et al. 2003). These conditions may limit the ability of parents to perceived differences in coloration among eggs. It is not known whether bluebirds, or other cavity nesters, can detect fine differences in egg color in a cavity. Future research should attempt to test whether a given bird species is capable of detecting the differences in coloration among eggs resting on nesting material in a cavity.

One hypothesis to explain the evolution of condition-dependent egg coloration is that egg coloration acts as a signal of condition or genetic quality of females to their mates (Moreno and Osorno 2003), and that female antioxidant capacity, immune response, and egg contents should also correlate with egg coloration. Indicator models of sexual selection propose that sexually selected traits signal specific aspects of individual quality (Andersson 1994). The differential allocation hypothesis (Burley 1986) predicts that males will invest more effort in raising the offspring of higher quality females. Perhaps assessing egg coloration enables males to make strategic reproductive decisions. Although little research has focused on the potential signaling function of egg coloration in the pied flycatcher, young hatched from more colorful blue eggs receive greater paternal care (Moreno et al. 2004) and have stronger humoral immune systems (Moreno et al. 2005). Further, the comparative analysis of Soler et al. (2005) regarding passerine birds found positive relationships between the extent of blue and green egg brightness and both duration of the nestling period and degree of parental care. To conclusively test the signaling hypothesis, experimental manipulations are needed that separate parental condition from egg coloration.

Another hypothesis to explain the evolution of distinctive and condition-dependent egg coloration of individual females is that such coloration facilitates discrimination of eggs from those laid by a brood parasite (Davies and Brooke 1988; Møller and Petrie 1991). Eastern bluebirds experience relatively high levels of conspecific brood par-

asitism (up to 10% of offspring; Gowaty and Karlin 1984) and occasionally reject what appear to be normal eggs by moving them to the periphery of the nest (L.S., personal observation). Experimental manipulations of nest site availability indicate that female bluebirds that are unable to acquire their own nesting cavities parasitize the nests of conspecifics (Gowaty and Bridges 1991). Condition-dependent egg coloration may facilitate egg discrimination if females in lower condition are less likely to secure nesting cavities, and therefore, are more likely to parasitize the nests of high condition females. Future research should address the ability of bluebirds to recognize brood-parasitic eggs by assessing egg coloration.

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