



The separate effects of egg size and parental quality on the development of ornamental plumage coloration

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The fitness-related consequences of egg size, independent of the influences of parental quality, are poorly understood in altricial birds. Not only can egg size and parental quality influence growth and survival, but each could influence the development of condition-dependent plumage coloration in offspring. The Eastern Bluebird *Sialia sialis* is an altricial, multi-brooded, cavity-nesting passerine in which juveniles display dichromatic UV-blue plumage. Previous research suggests that plumage coloration acts as a signal of individual quality among juvenile and adult Eastern Bluebirds. Here, we separate the effects of egg size and parental quality (defined by egg size laid) on nestling growth and plumage ornamentation by exchanging clutches of large eggs with clutches of small eggs. Nestlings were significantly larger immediately post-hatching when hatched from a large egg, but to maintain a larger size, nestlings needed to have hatched from a large egg and to have been reared by high-quality parents. Nestlings were brighter when reared by high-quality parents and this relationship was strongest later in the breeding season. Nestlings exhibited greater UV chroma if hatched early in the season, but UV chroma was not significantly affected by egg size or parental quality. These findings demonstrate varying influences of both egg size and parental quality on offspring growth and plumage ornamentation but suggest that quality of post-hatching investment is more influential than pre-hatching investment.

Keywords: growth, ornamental coloration, post-hatch investment, pre-hatch investment, sexual selection, structural coloration.

Across a broad range of oviparous animals, offspring hatched from large eggs experience fitness benefits. Larger eggs allow increased deposition of water, proteins or lipids and can provide offspring with greater post-hatch energetic reserves. Larger eggs produce enhanced immunity and lead to larger offspring and faster growth, all of which contribute to higher juvenile survival, an important component of fitness (reviewed in Williams 1994, Krist 2011). Wagner and Williams (2007) demonstrated that experimental reduction in egg size negatively influenced offspring survival and growth.

Little is known about the effects of egg size on sexually selected traits, such as ornamentation. Recent studies have started to investigate the role of egg composition (e.g. yolk hormones) in the development of sexually selected traits (Rubolini *et al.* 2006, Muller & Eens 2009, Bonisoli-Alquati *et al.* 2011), but none has examined the relationship between egg size and ornamentation. The early occurrence and development of sexual dichromatism have rarely been investigated in birds (reviewed in Kilner 2006). However, early resource availability could clearly influence the development of condition-dependent traits. Structural coloration, such as UV-blue plumage, is produced by the controlled absorption and scattering

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of light by feather nanostructure (Shawkey *et al.* 2003). However, if stress is experienced during growth of these tissues, the nanostructure pattern may be disrupted, reducing the refractive properties of the plumage (McGraw *et al.* 2002, Shawkey *et al.* 2003). Indeed, structural coloration varies with food availability and parasite loads, suggesting that this is a condition-dependent trait (McGraw *et al.* 2002, Hill *et al.* 2004, Siefferman & Hill 2005a, 2007). Therefore, egg size and resource availability during pre-natal development have the potential to create variation in structural plumage traits.

The influence of egg size per se on offspring quality can be difficult to quantify in animals with extensive post-hatch parental care behaviour. In altricial birds, offspring have higher survival rates when they hatch from larger eggs (Williams 1994), but also when their parents provision them more often (Clutton-Brock 1991). It stands to reason that parents capable of laying larger eggs are also capable of providing better care. Although variation in egg size remains poorly understood (Christians 2002), positive relationships in many species have been found between egg size and maternal age (Wiggins 1990, Croxall *et al.* 1992, Weimerskirch 1992, Robertson *et al.* 1994), condition (Galbraith 1988, Smith *et al.* 1993, Johnson *et al.* 2006), experience (Weimerskirch 1990, Thompson & Hale 1991, Sydeman & Emslie 1992) and nestling rearing abilities (Reid & Boersma 1990, Bolton 1991, Blomqvist *et al.* 1997, Risch & Rohwer 2000). Due to the interrelated nature of egg size and parental quality, early studies were unable to parse the separate contributions of egg size and parental quality on nestling survival and performance. However, clutch-swapping experiments allow the independent effects of egg size and parental quality to be examined (Magrath 1992, Smith *et al.* 1995, Amundsen *et al.* 1996, Krist 2009, reviewed in Krist 2011).

The Eastern Bluebird *Sialia sialis* is a multi-brooded, socially monogamous cavity-nesting passerine that produces altricial young. Juvenile Eastern Bluebirds express sexually dichromatic ultraviolet (UV)-blue coloration on their wings and tails, and retain these feathers to display in their first breeding season (Gowaty & Plissner 1998). Blue coloration is likely to be a sexually selected trait in this species because more colourful males and females have higher reproductive success (Siefferman & Hill 2003, 2005a). Thus,

the Eastern Bluebird offers an opportunity to study the separate effects of egg size and parental quality on nestling ornamentation and growth.

In this study, we use a clutch manipulation experiment to swap entire clutches of large eggs with clutches of small eggs to test the independent effects of egg size and parental quality on nestling growth and plumage colour. As with previous experiments (Amundsen & Stokland 1990, Reid & Boersma 1990, Amundsen *et al.* 1996), we assume that the ability to lay large eggs is associated with superior condition. Indeed, previous work with bluebirds demonstrates that females in better body condition lay larger eggs (Johnson *et al.* 2006, Robinson *et al.* 2010). Moreover, we assess whether seasonal variation (early vs. late breeding attempts) affects the relative influence of parental quality and egg size on measures of nestling quality.

METHODS

General field methods

During the 2004 breeding season (April–August), we monitored 200 Eastern Bluebird nestboxes in Craighead County, Arkansas, USA (35°54'N, 90°40'W). We visited nestboxes with complete clutches daily and recorded the date that the first egg was laid. During late incubation, we captured adults using a nestbox trap (Robinson *et al.* 2004) and marked them with unique combinations of colour bands for later identification. We recorded the age of birds that were recaptured from previous years (second-year vs. after-second year). We monitored the first and second clutches of every female and recorded the mean egg size for each clutch. For a subset of nests, parental feeding rates to offspring were measured when nestlings were 7 days old. Sony (New York, NY, USA) video cameras recorded parental activity for four continuous hours between 06:00 and 11:00 h and visits were quantified as the number of provisioning trips per hour.

We calculated a proxy of egg size by measuring the length and breadth of each egg (± 0.01 mm) with dial callipers and used the formula developed by Hoyt (1979), where mass (g) = $K * L * B^2$ (L = length (mm), B = breadth (mm), $K = 5.41 \times 10^{-4}$). We calculated the species-specific constant K by measuring a subset of 31 eggs to the nearest 0.001 g within 2 h of being laid using a portable electronic scale (Acculab PP2060D, Edgewood, NY, USA). Eggs weighed

for the constant calculation were distributed throughout the laying sequence and only one egg was weighed per clutch. Predicted egg mass by linear volume measurements is an accurate predictor of actual egg mass (Robinson *et al.* 2010).

Clutch manipulation protocol

We monitored nests until the total clutch was laid (usually four to five eggs). We exchanged whole clutches of large eggs (upper ~25% of the size distribution) with small eggs (lower ~25% of the size distribution) to separate the effects of pre-hatch and post-hatch investment on nestling performance (Nisbet 1978, Reid & Boersma 1990, Bolton 1991, Risch & Rohwer 2000). In this way, low-quality females (defined as those that lay small eggs) reared nestlings hatched from large eggs and vice versa. To control for the effect of egg swapping, we also exchanged clutches of large eggs with large eggs and small eggs with small eggs. We swapped eggs the day before hatching. The swap took no longer than 30 min and nest-holes were blocked so parents would not find an empty nest.

Nestling growth and coloration

Upon hatching, we uniquely marked nestlings with coloured permanent markers. We measured nestling mass on days 1, 3, 6, 9, 12 and 15 (± 0.01 g) with a digital scale between 08:00 and 12:00 h. When nestlings were 15 days old, we collected a 3-cm sample of the distal end of the fourth primary from the left and right wing for spectrophotometric analysis. We placed the feathers on black paper and stored the samples in dark, climate-controlled conditions until analysis. We conducted spectral analyses according to the general methods detailed in Siefferman and Hill (2007) using a USB 2000 spectrometer (range 250–880 nm, Dunedin, FL, USA) by holding a micrometre fibre-optic probe at a 90° angle to the feather surface. To smooth the curve, each reading was constructed from a mean of 20 reflectance curves. We recorded five readings from each feather, moving the probe as to not overlap a previous reading and then averaged the readings from the left and right primaries. We calculated brightness, or the total amount of light reflected by the feather, as the total area under the reflectance curve from 300 to 700 nm and UV chroma as the proportion of the total reflectance in the UV range ($\int_{300-400} / \int_{300-700}$). We determined nestling sex

by examining the amount of blue in emerging flight feathers (Pinkowski 1975); this method has been validated using molecular sexing techniques (Siefferman & Hill 2007).

Data analysis

We used SPSS (ver. 17.0; SPSS, Inc., Chicago, IL, USA) to analyse data with two-tailed tests for all analyses. We confirmed normality of residuals using Shapiro–Wilk tests. Unless otherwise mentioned, all means are followed by the standard error.

For the subset of nests at which we had recorded provisioning rates, we used backwards stepwise regression to investigate the effects of egg size and hatch date on provisioning rates. For the subset of females that were of known age (second-year and after second-year) and for which we had measured egg size over multiple years (2003 and 2004), we used a paired *t*-test to determine whether the egg size of individual females increased with age.

We used linear mixed models to determine whether nestling plumage coloration (brightness and UV chroma) was influenced by egg size or parental quality. We used a mixed model to test nestling growth using age (days 1, 3, 6, 9, 12 and 15 post-hatch) as the repeated measure and nestling ID as the subject. The fixed effects tested in each model included egg size (small and large), parental quality (low and high), breeding period (early- and late-season) and sex. Additionally, we included nestling age as a fixed factor in the repeated measures model. The covariate in each model was brood size. The random effect tested in each model was the ID of the rearing females.

The mixed model selection criterion we used was the likelihood ratio test (LRT) to determine whether random and main effects significantly improved the model fit and therefore should be incorporated. To do this, the difference in the -2 log likelihood score between the initial model and the model plus or minus the effect being tested is treated as a chi-square value with degrees of freedom equal to the number of parameters changed (Pinheiro & Bates 2000, West *et al.* 2007). Both forward and backward model selection procedures created the same model and only chi-square values from forward selection procedures are presented. Therefore, negative chi-square scores indicate a better model fit and positive chi-square scores indicate a poorer model fit. Furthermore, we

tested all interactions and only those with $P < 0.1$ were included in the model.

RESULTS

Provisioning rates for 50 pairs were recorded. Parental provisioning rates were influenced by both average egg size and day of year (overall model: $R^2 = 0.33$, $F_{2,48} = 11.70$, $P = 0.001$; Egg size: $\beta = 1.39$ (0.96); Day of year: $\beta = -0.05$ (0.01); Fig. 1). Pairs that laid larger eggs fed offspring more often and provisioning rates decreased during the breeding season. Individual females did not lay larger eggs when they were older (mean change \pm se: 0.02 ± 0.03 ; paired $t = 0.63$, $P = 0.54$; $n = 14$).

Forty-seven clutches of eggs were cross-fostered (26 early-season clutches and 21 late-season clutches). A linear mixed model indicated that nestlings hatching from larger eggs ($17.11 \text{ g} \pm 0.11$) were significantly larger than nestlings from small eggs ($16.82 \text{ g} \pm 0.11$; Table 1). However, there was a significant interaction between egg size and parental quality, indicating that nestlings hatched from large eggs were heavier on day 1 post-hatch regardless of parental quality, but to maintain a larger size throughout development, they also needed to be reared by high-quality parents (Table 1, Fig. 2). Whereas there was a non-significant trend for nestlings to be larger at any given age with greater parental quality, there was a significant interaction between parental quality and age such that

parental quality had a greater influence on older nestlings. Parental quality had little effect on nestlings until they reached day 6 post-hatch, a period of rapid growth, in which those with greater parental quality were larger (Table 1). Nestling sex and age also predicted mass; nestling mass increased with age, and male mass ($17.05 \text{ g} \pm 0.10$) was significantly greater than female mass ($16.87 \text{ g} \pm 0.10$; Table 1).

Nestlings were significantly brighter if they were male (male: 0.14 ± 0.002 , female: 0.12 ± 0.002), hatched during the late-season period (late-season: 0.14 ± 0.003 , early-season: 0.12 ± 0.003), and reared by high-quality parents (high-quality: 0.14 ± 0.003 , low-quality: 0.13 ± 0.003 ; Table 2, Fig. 3). However, there were significant interactions between breeding period and parental quality and breeding period and sex. Parental quality more strongly influenced brightness in late-season clutches (nestlings were brighter if they had high-quality parents in late-season clutches) and sex more strongly influenced brightness in early-season clutches (female brightness was negatively affected to a greater degree in early-season clutches).

Nestlings had a significantly greater UV chroma if they were male (male: 0.32 ± 0.002 , female 0.29 ± 0.002) and if hatched in the early-season (early-season: 0.31 ± 0.002 , late-season: 0.30 ± 0.002 ; Table 2). There was a non-significant interaction that remained in the model between breeding period and parental quality that indicated parental quality had a slightly more negative influence on UV chroma in the early-season broods.

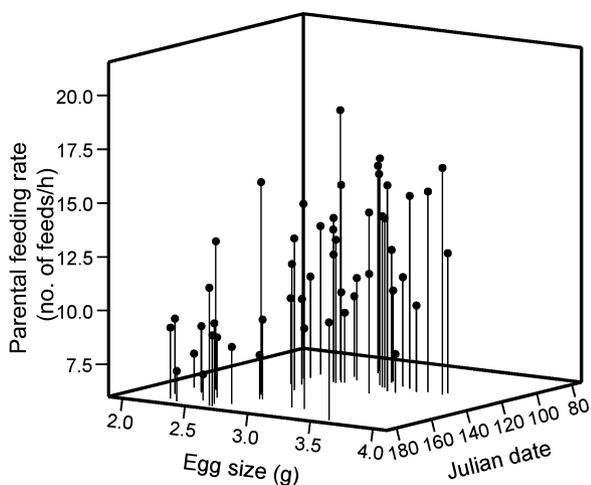


Figure 1. Relationship between average egg mass (g), parental provisioning rates to Eastern Bluebird nestlings (feeds per hour) and day of year (Julian).

DISCUSSION

This clutch-swapping experiment was designed to elucidate and separate the effects of egg size and parental quality on nestling growth and plumage ornamentation. Hatching from larger eggs significantly improved nestling mass immediately post-hatching, but this was only maintained throughout development when nestlings that hatched from larger eggs were also reared by high-quality parents (i.e. large-egg foster parents). High-quality parents also reared brighter nestlings in the late-season. Parental quality and egg size did not seem to influence UV chroma, which was only significantly influenced by breeding period and sex of the nestling.

Our data suggest that egg size influences offspring mass; nestlings hatched from larger eggs were

Table 1. Repeated-measures linear mixed model examining effects of egg size and parental quality on body mass in nestling Eastern Bluebirds.

	df	Estimate (se)	F/ χ^2	P
Variables included				
Intercept	56.76	3.11 (0.15)	30917.30	<0.001
Egg size ^a	92.15	0.57 (0.16)	6.33	0.01
Parental quality ^b	95.10	0.13 (0.20)	3.65	0.06
Sex ^c	118.57	0.18 (0.07)	6.79	0.01
Age ^d	259.62	3 = 3.04 (0.14)	9933.49	<0.001
		6 = 12.66 (0.29)		
		9 = 21.03 (0.25)		
		12 = 25.07 (0.26)		
		15 = 24.60 (0.26)		
Egg size*Parental quality	102.28	0.56 (0.22)	6.14	0.02
Parental quality*Age	261.02	3 = 0.27 (0.19)	3.42	0.01
		6 = 1.42 (0.39)		
		9 = 0.28 (0.35)		
		12 = 0.46 (0.36)		
		15 = 0.53 (0.36)		
Variables excluded				
Brood size			1.45	0.23
Breeding period			2.18	0.14

Female ID was the random effect (variance estimate = 0.18 ± 0.06). The test statistic for variables in the model is F and it is χ^2 for factors excluded from the model. For the variables excluded, none makes the model significantly better (more negative χ^2) when added using forward selection procedures. ^aEstimates are relative to small egg size. ^bEstimates are relative to low parental quality. ^cEstimates are relative to females. ^dEstimates are relative to day 1 post-hatch.

larger at day 1 post-hatch regardless of parental quality. However, nestlings hatched from small eggs quickly caught up in growth by day 3 post-hatch. Only nestlings hatched from a large egg and reared by high-quality parents maintained a significantly higher mass up to fledging age (day 15). Nestlings hatching from large eggs are typically heavier at hatching (Amundsen & Stokland 1990, Reid & Boersma 1990, Magrath 1992), mostly likely because they possess greater energetic reserves than those hatching from small eggs (Williams 1994). Once nutrient reserves are depleted, though, it would be logical for mass to be influenced by parental care alone. Therefore, it is interesting that we found enhanced mass only when nestlings were both reared by high-quality parents and hatched from large eggs, as opposed to all nestlings reared by high-quality parents. This suggests not only that there is a lingering beneficial effect of egg size but that parents that lay large eggs also rear larger nestlings. The positive correlation between egg size and parental provisioning rates suggests that increased feeding rates could cause nestlings to grow larger. Other studies have also found that effects of parental quality are only evident in older nestlings and this could be because the influence of parental

quality is additive (Reid & Boersma 1990, Magrath 1992). Although we did not measure recruitment of offspring into the breeding population in subsequent years, survival probabilities are expected to be greater for larger offspring, thus positively influencing fitness. For example, Common Starlings *Sturnus vulgaris* with greater mass at fledging experience higher post-fledging survival and recruitment (Smith & Bruun 1998).

To our knowledge, this is the first experimental test of the separate influences of egg size and parental quality on a sexually selected trait. Our experiment demonstrates that parental quality significantly influences nestling feather brightness regardless of egg size, but only in late-season nestlings. These data are consistent with results that show that low food availability (low-quality parental care) causes adverse effects to feather brightness (Siefferman & Hill 2007, Doyle & Siefferman 2014). Moreover, this is the first study to demonstrate that environmental factors predict variation in ornamentation of female offspring. Female brightness was negatively impacted to a greater extent early in the season.

It is interesting that we were only able to detect the effect of parental quality on nestling brightness

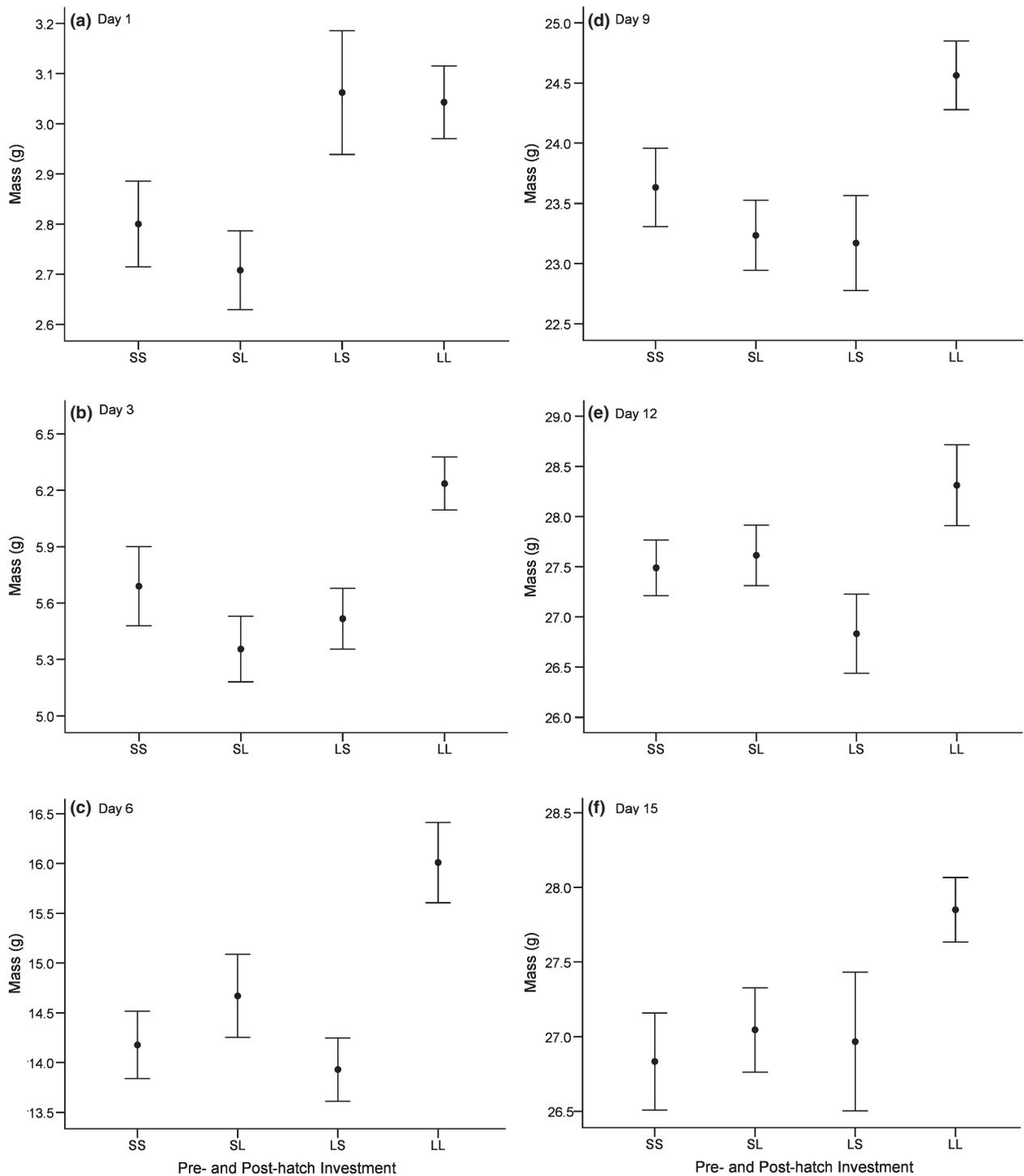


Figure 2. Effects of pre- and post-hatching investment on nestling mass on (a) day 1, (b) day 3, (c) day 6, (d) day 9, (e) day 12 and (f) day 15 post-hatch. Nestlings were exposed to small egg and small-egg foster mother (SS), small egg and large-egg foster mother (SL), large egg and small-egg foster mother (LS), or large egg and large-egg foster mother (LL). Error bars represent \pm se.

Table 2. Linear mixed model testing effects of egg size and parental quality (PQ) on Eastern Bluebird nestling plumage coloration.

Model	df	Estimate (se)	F/ χ^2	P
Brightness				
Variables included				
Intercept	20.62	0.16 (0.004)	4726.72	<0.001
Egg size ^a	39.55	0.001 (0.003)	0.03	0.86
Parental quality ^b	30.82	0.02 (0.005)	5.88	0.02
Sex ^c	116.23	0.009 (0.004)	42.51	<0.001
Breeding period ^d	47.51	0.02 (0.005)	27.88	<0.001
PQ*Breeding period	49.53	0.02 (0.007)	11.83	0.001
Sex*Breeding period	115.56	-0.01 (0.005)	7.55	0.01
Variables excluded				
Brood size			8.08	0.004
UV Chroma				
Variables included				
Intercept	26.27	0.31 (0.004)	31748.08	<0.001
Egg size ^a	48.84	0.001 (0.003)	0.05	0.82
Parental quality ^b	39.86	-0.008 (0.004)	0.78	0.38
Sex ^c	119.61	0.03 (0.002)	245.65	<0.001
Breeding period ^d	57.47	-0.01 (0.004)	10.07	0.002
PQ*Breeding period	63.12	-0.01 (0.006)	2.94	0.09
Variables excluded				
Brood size			8.63	0.003

Female ID was the random effect in all analyses (variance estimates: Brightness = 0.0001 ± 0.00003 ; UV chroma = 0.0001 ± 0.00002). The test statistic for variables in the model is F and it is χ^2 for factors excluded from the model. For the variables excluded, none makes the model significantly better (more negative χ^2) but rather significantly worse (more positive χ^2) when added using forward selection procedures. ^aEstimates are relative to small egg size. ^bEstimates are relative to low parental quality. ^cEstimates are relative to females. ^dEstimates are relative to early-season.

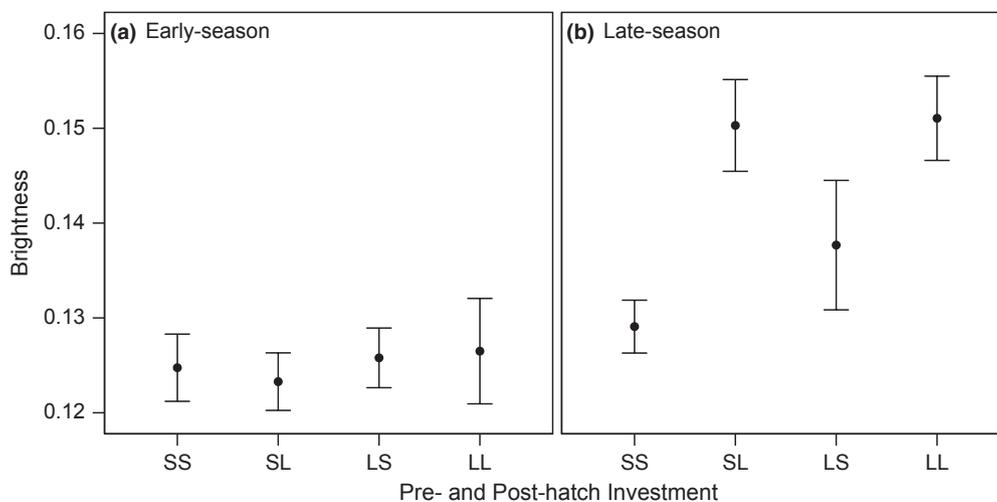


Figure 3. Influence of pre- and post-hatching investment on brightness in (a) early- and (b) late-season nestlings. Nestlings were exposed to small egg and small-egg foster mother (SS), small egg and large-egg foster mother (SL), large egg and small-egg foster mother (LS), or large egg and large-egg foster mother (LL). Error bars represent \pm se.

in the late-season nestlings. Perhaps the condition dependence of this colourful trait is best revealed under more stressful environments. In multi-brooded passerines, environmental conditions often

differ between breeding attempts; therefore, both nestlings and females may change their investment strategies with changes in selection pressures. In our population and others, later in the breeding

season, nestling Bluebirds are provisioned less often but are fed larger food items (T. Robinson unpubl. data, Siefferman & Hill 2007). Thus, although environmental conditions change with season, it is not clear that conditions deteriorate as the season progresses.

Nestling coloration is likely to influence future reproductive success of Eastern Bluebirds. The UV-blue structural plumage coloration of male and female Eastern Bluebirds is probably a sexually selected trait; more colourful adults produce more offspring and feed offspring more often (Siefferman & Hill 2003, 2005a). Conspecifics may also use plumage coloration to mediate competitions for breeding territories (Siefferman & Hill 2005b). Because coloration is associated with resource-holding potential, our data suggest that nestlings hatched in high-quality natal environments may gain advantages in future reproductive success. Additionally, the plumage coloration of juvenile Bluebirds may serve as an honest signal of quality to parents or among juveniles. Variation in brightness of offspring appears to influence parental favouritism in this species; experimental manipulations of nestling coloration demonstrate that fathers preferentially feed and protect sons that have been experimentally brightened, over sons that have been experimentally dulled (Ligon & Hill 2010, Barrios-Miller & Siefferman 2013).

Our results demonstrate the independent effects of variation in pre- and post-hatch investment on nestling growth and ornamentation. As we swapped clutches of large eggs with clutches of small eggs, we argue that the impacts of pre-hatch investment on nestling traits are likely to be a consequence of egg size. Because we found no effect of female age on egg size, it is unlikely that maternal age confounds the effects of egg size on nestling characteristics. However, a large egg could also be a high-quality egg (Williams 1994), and thus other components of egg quality may influence growth and ornamentation of nestlings. In birds, mothers influence the fitness of offspring through the differential deposition of various egg constituents, including androgens (Schwabl 1993) and antioxidants (Royle *et al.* 2001). Thus, we cannot rule out the possibility that other components of egg quality may influence nestling growth and ornamentation. The effects on ornamentation were only discerned during the second breeding period, suggesting that environmental conditions (e.g. food availability and/or quality) mediate

relationships between egg quality, parental quality and offspring fitness. Overall, post-hatching investment influenced plumage coloration, suggesting that egg size has little effect on ornamentation in this species.

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