Supplemental food increases ornamentation of male nestling Eastern Bluebirds

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ABSTRACT. Although the condition-dependence and signaling function of ornamental plumage coloration among adult males is well studied, less research has focused on the information content of ornamental coloration among juvenile birds. Eastern Bluebird (*Sialia sialis*) nestlings grow their nuptial plumage while in the nest and dependent on parents for food, making them an ideal species for studying the development and function of elaborate plumage. Previous research suggests that plumage brightness of Eastern Bluebirds functions, in the juvenile stage, in parent–offspring interactions as a sexually selected trait in adults. Using an experimental approach, we tested the effects of supplemental food on the structural plumage coloration (i.e., tips of primary feathers) of Eastern Bluebird nestlings in Watauga County, North Carolina, during the 2011 breeding season. We provided supplemental mealworms daily to breeding pairs from the onset of incubation through the nestling period, and measured plumage brightness, UV chroma, and mass of nestlings ($N = 89$ males and 71 females). Male nestlings of supplementally fed parents exhibited brighter plumage. The mass and UV chroma of young bluebirds were not significantly affected by food supplementation. However, the relationship between mass and brightness differed between male nestlings in the control and supplementally fed treatments. Males reared in food-supplemented territories exhibited a positive relationship between color and mass. Nestlings in control territories, however, exhibited a negative relationship between size and brightness, suggesting that reduced food availability results in a tradeoff between allocating resources toward somatic growth and development of bright plumage. Our results suggest that UV-blue structural plumage in male juvenile Eastern Bluebirds is at least partially condition-dependent and may help to explain why plumage color can influence social interactions in Eastern Bluebirds.

RESUMEN. **El alimento suplementario aumenta la ornamentación de los pichones macho del Azulejo Graganta Canela**
A pesar de que la función condición-dependiente y de señalización del plumaje ornamental entre machos adultos está bien estudiado, pocos estudios se han focalizado en el contenido de información de la coloración entre las aves juveniles. Los juveniles de Azulejo Garganta Canela (*Sialis sialis*) obtienen su plumaje nupcial mientras aún están en el nido y dependen de sus padres para alimentarse, haciéndolos especies ideales para el estudio del desarrollo y la función del plumaje elaborado. Estudios anteriores sugieren que el brillo del plumaje del Azulejo Garganta Canela funciona, en el estadio juvenil, en las interacciones paterno-filiales como un carácter sexualmente seleccionado en adultos. Utilizando esta aproximación, pusimos a prueba el efecto del suplemento alimentario en la coloración estructural (i.e., puntas de las plumas primarias) de juveniles del Azulejo Garganta Canela en el condado de Watauga, Carolina del Norte, durante la temporada reproductiva de 2011. Proveímos diariamente de un suplemento de gusanos a parejas reproductivas desde el inicio de la incubación, y medimos el brillo del plumaje, el UV croma, y la masa de los juveniles ($N = 89$ machos y 71 hembras). Los juveniles de padres que habían sido suplementados exhibieron un plumaje más brillante. La masa y el UV croma de los juveniles de azulejo no fue significativamente afectada por la suplementación alimentaria. Aún así, la relación entre la masa y el brillo difirió entre juveniles de los tratamientos control y alimentados suplementariamente. Los machos criados en territorios con alimento suplementario exhibieron una relación positiva entre el color y la masa. Los juveniles en los territorios control, sin embargo, exhibieron una relación negativa entre el tamaño y el brillo, sugiriendo que la reducción en la disponibilidad de alimento resulta en un intercambio entre la alocación de recursos hacia el crecimiento somático y el desarrollo del plumaje brillante. Nuestros resultados sugieren que el plumaje estructural UV-azul en los machos juveniles del Azulejo Garganta Canela está al menos parcialmente condicionado y puede ayudar a explicar por qué el color del plumaje puede influenciar las interacciones sociales en el Azulejo Garganta Canela.

Key words: condition dependent, juvenile ornamentation, plumage coloration, *Sialia sialis*, supplemental food

Elaborately colored males often experience high reproductive success, whether by acquiring the best breeding resources or by being more attractive to females (Hill and McGraw 2006). The role of plumage coloration, however, has focused almost exclusively on these adult intra- and intersexual interactions; the function of elaborate plumage coloration during the fledgling stage is poorly understood (Kilner 2006).

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The feathers of most juvenile birds, especially those of precocial species, are dense down or downy tufts that are replaced with ornamented feathers in adulthood (Kilner 2006). However, some altricial species possess bright plumage in early development, for example, rails (family Rallidae; Kilner 2006). Because altricial juveniles often compete for their parents' attention, plumage characteristics can serve as signals of offspring need or quality to parents. For example, American Coot (*Fulica americana*) parents preferentially feed chicks with brighter head plumes (Lyon et al. 1994), and Great Tit (*Parus major*) nestlings with brighter yellow nape patches are fed more often by parents (Gálvan et al. 2008). This favoritism can be demonstrated by such simple provisioning decisions or, in some extreme cases, by selective brood reduction, for example, European Coot (*Fulica atra*; Horsfall 1984).

Parents that exhibit favoritism toward particular offspring should experience higher fitness when they invest more in the highest-quality young. Offspring ornamentation, therefore, may be expected to honestly convey offspring quality. For example, larger nestling Blue Tits (*Parus caeruleus*; Johnsen et al. 2003) and those reared in smaller broods (Jacot and Kempenaers 2007) exhibit more-colorful blue plumage, and Common Moorhen (*Gallinula chloropus*) chicks with more colorful bills tend to be larger (Fenoglio et al. 2002).

Indicator models of honest signaling propose that the expression of ornamental traits should be correlated with individual condition (Andersson 1994). If only exceptionally fit individuals in a population can express the most elaborate traits, then these traits can reliably signal individual quality (Andersson 1994). Therefore, understanding how individual condition influences such traits is critical to understanding how these characteristics serve to maximize fitness. Yet, individual condition or quality is often defined vaguely in the literature. Recently, Hill (2011) defined condition as the relative capacity to maintain optimal functionality of essential cellular processes, or the capacity to withstand environmental challenges. There are many factors that contribute to condition, and condition itself may be divided into three discrete components: somatic state, genotype, and epigenetic state (Hill 2011). For example, stored resources and energy reserves can play a vital role in cellular functionality and the somatic state of the animal (Hill 2011).

Eastern Bluebirds (*Sialia sialis*) are cavity-nesting, socially monogamous dichromatic songbirds. Males have blue-ultraviolet coloration on their heads, backs, wings, and tails whereas females exhibit duller blue-ultraviolet coloration. In juveniles, the sexually dichromatic blue plumage of primary wing feathers and rectrices develops while they are still in the nest, ~11 d after hatching. When nestlings are 14 d old, plumage coloration can be quantified (Siefferman and Hill 2007). During late summer and into the fall, young bluebirds molt into their nuptial plumage, but only replace their body feathers, retaining the blue wing and tail feathers grown while in the nestling and fledgling stages (Siefferman and Hill 2007).

Recent studies of function of ornamental coloration in juvenile Eastern Bluebirds suggest that it functions as a signal to parents. Fathers preferentially defend brighter over duller sons from mock predators (Barrios-Miller and Siefferman 2013). Moreover, when resources are limited, parents preferentially feed experimentally brighter over duller offspring (Ligon and Hill 2010). The UV-blue plumage coloration may also serve a signaling function in adult Eastern Bluebirds. Brighter blue males tend to gain access to better nesting territories than duller males (Siefferman and Hill 2005) and more-colorful males experience higher reproductive success (Siefferman and Hill 2003). Thus, the wing and tail plumage that bluebirds develop during the juvenile period may function as a signal to conspecifics during both the juvenile and adult stages.

The blue structural coloration of juvenile Eastern Bluebirds may be influenced by natal environment. Using a brood-size manipulation experiment, Siefferman and Hill (2007) showed that male nestlings reared in reduced broods (less crowded conditions) grew brighter blue wing feathers than those reared in enlarged (more crowded) broods. How crowded conditions reduce plumage brightness is not understood, but availability of food during the nestling stage likely influences the development of UV-blue coloration in Eastern Bluebirds.

In this study, we investigated the relationship between individual condition and nestling ornamentation in Eastern Bluebirds using an experimental approach with supplemental food.

During the breeding season, we provided blue-birds with mealworms (*Tenebrio molitor*) and measured nestling coloration and body mass and investigated relationships between mass and plumage coloration during the nestling period of rapid growth. We predicted that offspring given supplemental food would display brighter blue plumage and also predicted that, if food was limited, control nestlings would weigh less than experimental nestlings. Moreover, in control nests, where food resources are likely more limited, we expected nestlings to experience tradeoffs between developing bright coloration and skeletal growth (sensu Hill 2011). In experimental nests, however, we expected that individual condition would either covary positively with plumage brightness or not be statistically related to brightness.

METHODS

Field site and general methods. We monitored 180 nest boxes in Watauga County, North Carolina (36°11′39″N, 81°44′5″W), during the 2011 breeding season (April–July). We recorded dates of nest construction, first egg, and hatch. Upon hatching (mean brood size = 4.0 ± 1.0 [SD] nestlings), we uniquely marked each nestling on the tarsi with Sharpie® markers (red, blue, or green). We measured the mass of nestlings (±0.1 g) at 2, 5, 8, 11, and 14 d post-hatching (hatch day = 1). When 8 d old, we fitted nestlings with U.S. Geological Survey (USGS) aluminum bands. In addition, parents were captured and banded with unique four-color leg bands and a USGS band, and eight feathers were taken from the UV-blue rump region of each adult.

When nestling were 14 d old, we took feather samples. Nestlings fledge between 15 and 20 d after hatching at our study site. Nestlings have feather sheaths when 8 d old and, by 14 d old, 2 cm of the primaries have emerged from the sheaths; if the feathers were not yet 2-cm-long, clipping was postponed 1–3 d. The fifth primary feather is the longest feather at this age, and left and right fifth primary feathers were cut (2 cm of the distal end) from each nestling for spectrophotometric plumage analyses. We classified male (*N* = 89) and female nestlings (*N* = 71) using sexually dichromatic plumage coloration. Previous experience with plumage coloration and molecular classification showed

that 95% of young could be properly classified using plumage coloration (L. Siefferman, pers. obs.).

In a subset of nests (control *N* = 14, experimental *N* = 16), we video-recorded parental provisioning rates when nestlings were 11 (±1 [SD]) d old, but did not record during inclement weather. We set up video cameras ~3 m from each nest box and recorded for 2 h between 09:00 and 12:00. We quantified provisioning trips and calculated provisioning rates as the mean number of provisioning trips by both parents per minute. Although all parents fed their young insects, we were unable to distinguish between different insects and insect larvae so we omitted prey identification from our analyses.

Plumage measurements. After clipping, feathers were stored in envelopes in a climate-controlled environment and then taped by the rachis to black non-reflectance paper, imitating how the feathers lie flat naturally on the bird. One researcher (A.D.) recorded spectral data with a spectrometer (range = 250–880 nm; Model S2000, Ocean Optics, Dunedin, FL, USA) using a micron fiber-optic probe placed at a 90° angle to the feather surface. For nestlings, plumage reflectance was measured ~2 cm from the distal end of the right and left primaries. We took two measurements from each feather, giving a total of four measurements per nestling. For adults, we measured plumage reflectance five times. Using the mean spectral data, we quantified color using two standard descriptors of reflectance spectra: mean brightness and UV chroma. Mean brightness was calculated as the mean of the summed reflectance 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; Siefferman and Hill 2007). We did not measure hue (wavelength of peak reflectance) because the spectral curves of nestlings are relatively flat (Siefferman and Hill 2007) and because, in adults, this measure is strongly correlated (and redundant) with UV chroma (Siefferman and Hill 2003).

Food supplementation experiment. We conducted a supplemental feeding experiment using mealworms (Camillies Vita-mealies®) reared on organic food. At the start of incubation, nests were randomly designated as supplemented or controls. We initially had 23 supplemented nests and 26 controls, but, due to abandonment (*N* = 8) and predation (*N* = 4),

our final sample sizes were 20 supplemented nests and 17 controls. We attached small plastic cups to the top of all experimental and control nest boxes. We visited both experimental and control nests daily (from the start of incubation until nestlings were 15 d old) and placed 15 g of mealworms in the cups of experimental nests. For the first 2 d that we supplementally fed experimental pairs, we observed parental responses to the food supplementation with binoculars to verify that the bluebirds were eating the mealworms, and to ensure that no other species were consuming them. All pairs began using the supplemental food within 2 d of the experiment and, thereafter, began eating the mealworms within 3 min of delivery and all were consumed by the next morning; no other birds were observed at supplemented nest boxes during this time. We observed adults to determine if they fed their young the supplemental mealworms. On days that we videotaped nests for parental feeding rates, supplemental food was not provided until after the recordings were complete.

Statistical analyses. To test the effect of supplemental food and nestling sex on nestling UV chroma and brightness, we ran separate general linear mixed effects models (GLMM) and used a repeated measures linear mixed model for nestling mass. Additionally, to determine if other confounding variables (parental provisioning rate, parental color, and brood size) affected offspring coloration and mass, we included these variables as covariates, but removed unimportant variables using a forward stepwise approach. Nest identity was the random factor; experimental treatment, nestling sex, parental provisioning rate, parental color, and brood size were listed as factors. We tested for all potential interactions, but because we found significant interactions ($P < 0.05$) between sex and many factors, we ran separate models for male and female nestlings. In models for both male and female nestlings, parental provisioning rate ($P > 0.70$), parental color (male and female brightness and chroma; all $P > 0.47$), and brood size ($P > 0.20$) did not contribute significantly to the models and, therefore, were excluded from analyses.

The repeated measures linear mixed model that tested the effect of supplemental food and sex on nestling mass had nest identity as the random factor and nestling identity as the repeated factor. For nestling mass, we found a significant interaction between treatment and nestling age ($P < 0.05$) so we ran separate mixed models for each age (2, 5, 8, 11, and 14 d post-hatching) to determine if treatment or nestling sex influenced mass. We used Student's t-tests to compare provisioning rates of experimental versus control nests. Finally, separately for male and female nestlings, we used ANCOVAs to test whether nestling sex and mass at 8 d post-hatching (when nestlings are growing the fastest; Table 1) influenced brightness. Because there was a significant interaction between mass and treatment ($P < 0.05$), we separated the nestlings by treatment and tested for relationships between mass and plumage brightness. SPSS Version 19.0 software (SPSS, Inc., Chicago, IL, USA) was used to analyze data and all tests were two-tailed, with the alpha level set at $P = 0.05$.

RESULTS

All adult Eastern Bluebirds that received supplemental food were observed eating mealworms and all parents were observed feeding mealworms to their young. In the subset of nests that were video-recorded, adult bluebirds at supplemented (mean $= 0.066 \pm 0.054$ [SD] provisioning trips/min) and control nests (0.055 ± 0.039 provisioning trips/min) fed nestlings at similar rates ($t = 0.20$, $P = 0.56$, $N = 30$).

Male nestlings were significantly heavier than females at ages 5, 11, and 14 d post-hatching (Tables 1 and 2). However, we found no significant effect of the supplemental treatment on the mass of either male or female nestlings at any age (Tables 1 and 2). Male nestlings of parents that received supplemental food exhibited brighter plumage (Table 3, Fig. 1). We detected no significant effect of food supplementation on UV chroma of the wing feathers of males and no effect of either color variable among female nestlings (Table 3).

For plumage brightness of 8-d-old male nestlings, we found a significant interaction between treatment and mass (ANCOVA: $F_{2,66} = 4.5$, $P = 0.014$). Thus, we divided the data set by treatment and ran separate linear regressions to test relationships between male mass and brightness. We found a significant positive relationship for male nestlings that were supplementally fed ($R^2 = 0.12$, $F_{1,37} = 5.0$, $P = 0.03$), but found

Table 1. Mean (SD) mass of 2-, 5-, 8-, 11-, and 14-d-old male and female Eastern Bluebird nestlings at nest boxes that either were (Supplemented) or were not (Control) provided with supplemental food.

Age (days)	Control males ($N = 43$)	Control females ($N = 26$)	Supplemented males ($N = 46$)	Supplemented females ($N = 45$)
2	3.7 (0.9)	4.1 (0.8)	4.1 (0.8)	4.0 (0.8)
5	10.6 (1.8)	10.9 (1.4)	11.4 (1.9)	11.2 (1.7)
8	16.9 (1.9)	20.0 (2.4)	19.4 (3.2)	19.6 (2.8)
11	26.6 (2.4)	25.3 (3.0)	25.8 (2.1)	25.8 (2.6)
14	27.4 (2.4)	26.2 (2.9)	27.2 (1.6)	27.1 (2.1)

Table 2. Effect of food supplementation and sex on mass of nestling Eastern Bluebirds at 2, 5, 8, 11, and 14 d post-hatching. None of the covariates contributed significantly to any model ($P > 0.20$) and thus were removed in a forward stepwise fashion.

Age	Factors	df	Est (SE)	F	P
2	Exp[a]	44.2	−0.18 (0.21)	0.7	0.39
	Sex[b]	173.6	0.03 (0.11)	2.1	0.13
5	Exp[a]	45.8	−0.60 (0.44)	1.8	0.18
	Sex[b]	140.8	−0.13 (0.24)	5.7	0.004
8	Exp[a]	46.6	−0.01 (0.74)	0.0	0.99
	Sex[b]	157.7	−0.01 (0.33)	2.1	0.12
11	Exp[a]	40.9	0.25 (0.68)	0.1	0.71
	Sex[b]	151.7	−0.54 (0.32)	3.3	0.04
14	Exp[a]	36.5	−0.19 (0.63)	0.1	0.75
	Sex[b]	56.2	−0.30 (0.24)	3.9	0.02

[a]Experiment was coded as 0 for control and 1 for supplemented.
[b]Sex was coded as 0 for female and 1 for male.

Table 3. Effect of food supplementation on nestling brightness and UV chroma of male and female nestling Eastern Bluebirds when ~14 d old. Factors that did not contribute to the model ($P > 0.20$) were removed in a forward stepwise fashion.

Trait	Sex	Factors	df	Est (SE)	F	P
Brightness (%)	M	Exp[a]	21.3	2.44×10^{-4} (1.67×10^{-4})	5.2	0.03
	F	Exp[a]	31.1	2.82×10^{-4} (1.58×10^{-4})	2.2	0.14
UV Chroma	M	Exp[a]	25.1	6.98×10^{-5} (4.18×10^{-5})	1.3	0.26
	F	Exp[a]	31.3	1.61×10^{-5} (1.41×10^{-5})	1.3	0.27
	F	Brood size	32.7	1.35×10^{-5} (1.35×10^{-5})	2.8	0.10

[a]Experiment was coded as 0 for control and 1 for supplement.

a significantly negative relationship between nestling mass and brightness of control nestlings ($R^2 = 0.17$, $F_{1,29} = 5.8$, $P = 0.02$; Fig. 2). Also, for plumage brightness of female nestlings, we found a significant interaction between treatment and mass (ANCOVA; $F_{2,55} = 3.4$, $P = 0.04$). The relationship between brightness and mass was not significant in either treatment (control: $R^2 = 0.00$, $F_{1,17} = 0.02$, $P = 0.97$; supplementally fed: $R^2 = 0.08$, $F_{1,39} = 3.2$, $P = 0.08$).

DISCUSSION

Our finding that supplementally fed male nestling Eastern Bluebirds developed brighter plumage is consistent with the hypothesis that structural coloration is, at least partially, condition-dependent. Of course, our food-supplementation experiment was an indirect manipulation of chick condition because the nutritional state of the chicks was not directly manipulated. Thus, treatment effects could be due to changes in the behavior of adults. Our
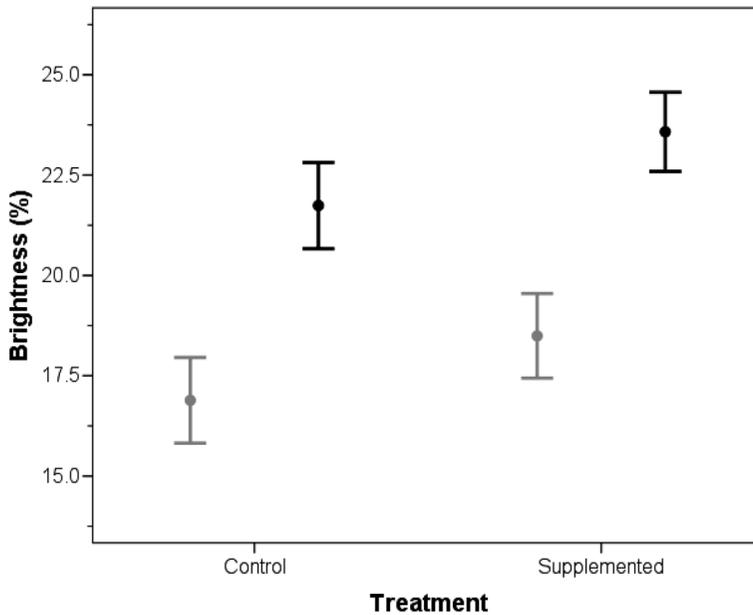
Fig. 1. Plumage brightness of 14-d-old male and female nestling Eastern Bluebirds at nest boxes that were (Supplemented) or were not (Control) provided with supplemental food. Gray bars represent females and black bars males. Data are presented as mean ± SE.

finding that supplementally fed male nestlings grew brighter plumage corroborates the findings of Siefferman and Hill (2007) and Jacot and Kempenears (2007), who found that male, but not female, nestling Eastern Bluebirds and Blue Tits reared in enlarged broods developed duller blue feathers than those reared in reduced broods. Moreover, blood protein levels correlate with blue structural coloration in male, but not female, nestling Blue Tits (Peters et al. 2007). These results suggest that female plumage is less adversely influenced by natal environment than male plumage. Sex differences in condition dependence may be indicative of sex differences in the costs of producing UV-blue coloration, the energy invested in somatic growth, or both.

We found that male Eastern Bluebirds exhibit more elaborate coloration that may be more costly to produce. Similar sexual dichromatism in juvenile coloration has been reported in Blue Tits (Johnsen et al. 2003) and Florida Scrub-Jays (Siefferman et al. 2008). Among bluebirds, there is likely stronger selection pressure on males than females to develop bright plumage because brighter blue-UV coloration appears to aid males in securing high-quality nesting

sites (Siefferman and Hill 2005). Moreover, we found sexual size dimorphism in nestling bluebirds, with males heavier than females at 5, 11, and 14 d post-hatching. Thus, males may experience greater energetic demands than females in both growth and development of bright plumage. An alternative explanation for the stronger effect of food supplementation on plumage of male nestlings is that supplementally fed parents may have fed males more often than females. Although we do not know if this was the case, previous research suggests that the begging rates of male and female nestling Eastern Bluebirds do not differ (Soley et al. 2011). In addition, although adult Eastern Bluebirds have been found to show favoritism for some older nestlings (at least 14 d old; Barrios-Miller and Siefferman 2013) and fledglings (Ligon and Hill 2010), they likely use plumage cues that are not apparent until young are about 14 d old.

Although parents on territories with supplemental food fed their young the mealworms, we detected no effect of supplemental food on the growth or final body mass of nestlings. These data suggest that the intrinsic quality of the habitat at our study site may have been sufficient
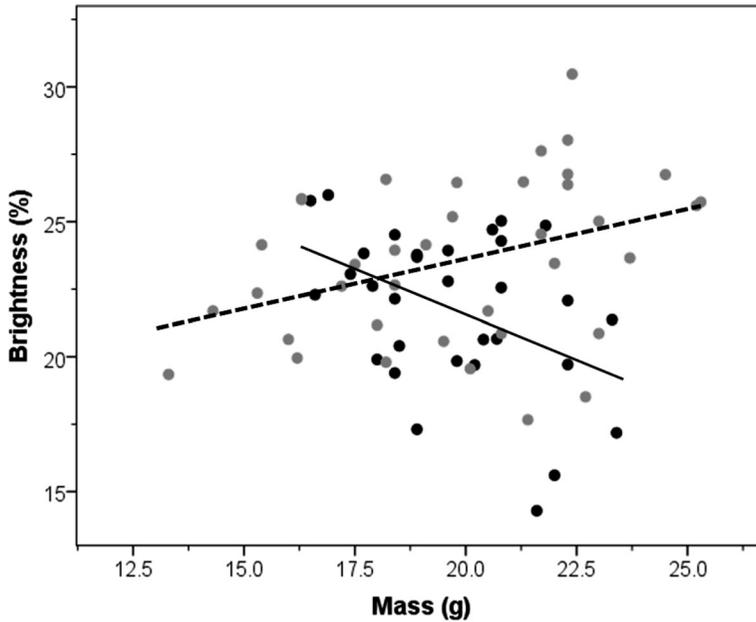
Fig. 2. Relationship between mass at 8 d post-hatching and plumage brightness of 14-d-old male Eastern Bluebirds at nest boxes that were or were not (control) provided with supplemental food. Gray circles (dashed line) represent supplementally fed nestlings and black circles (solid line) represent control nestlings.

to sustain the needs of growing nestlings. In addition, at fledging, young birds that are excessively heavy may have more difficulty flying before wing muscles are fully developed (Remeš and Martin 2002). Therefore, once growth requirements were met, extra energy may have been allocated to feather ornamentation.

For male nestlings, our data demonstrate that the relationship between mass at age 8 and feather brightness differed with treatment. Control nestlings that were heavier at 8 d post-hatching exhibited duller coloration at fledging; those males may have experienced a tradeoff in allocating energy toward growth and plumage brightness. The opposite relationship was found in male nestlings from territories with supplemental food; nestlings that were heaver at 8 d post-hatching exhibited brighter coloration. Among the supplementally fed nestlings, those in good condition, with highly functional cellular processes, could apparently invest in both growth and bright coloration. Young bluebirds exhibit the fastest nestling growth at 8 d post-hatching and when feather shafts are emerging from the dermis (Siefferman and Hill 2007). Unless food resources are abundant, male

nestlings likely must allocate energy toward growth or coloration. Our results further suggest that nestlings generally prioritize structural growth over development of bright plumage coloration. Although we are not aware of a similar experiment with other species, the UV-blue color of the tail of male Blue Tit nestlings was found to be negatively related to plasma protein concentrations (Peters et al. 2007). This suggests that male nestlings that withdrew more protein from circulation for feather manufacture were able to develop more colorful feathers and again points to tradeoffs between investing energy in growth and developing elaborate coloration.

The mechanism by which greater access to food increases plumage brightness (but not UV chroma) remains unclear. In bluebirds, variation in this non-iridescent blue-UV coloration is structurally based (Shawkey et al. 2003). Structural colors are produced by the arrangement of elements within the microstructure of a feather (Hill and McGraw 2006). UV-blue structural feathers are composed of a keratin cortex and a spongy medullary layer that consists of feather barbs and large central vacuoles surrounded by small granules of melanin (Shawkey et al. 2003).

Color arises due to the coherent scattering of light particles (Hill and McGraw 2006). Although structural colors have been found to be negatively affected by nutritional stress (Keyser and Hill 1999, Doucet 2002), suggesting that saturation of colors may depend on regularity of elements within the microstructure, how condition influences structurally based coloration remains poorly understood (Prum 2006). The differential effects of the food supplementation on nestling brightness and UV chroma in our study suggest that these two color descriptors arise from different pathways. For example, external feather features may influence feather brightness. Birds with thinner keratin cortexes tend to be brighter (Shawkey et al. 2003), and feather wear over time has been shown to decrease brightness (Surmacki et al. 2011). Clearly, we need a better understanding of how non-iridescent plumage coloration is developed and maintained.

Our data demonstrate that structural coloration of juvenile Eastern Bluebirds is, at least partially, dependent on condition. Although blue coloration appears to function in competition for nest sites among adult males (Siefferman and Hill 2005), bright plumage may also be an important signal to parents during the fledgling stage. After leaving nests, altricial young still depend on their parents for food for a short period of time, and visual cues such as feather ornamentation may aid parents in making strategic parental-care decisions. Indeed, both Ligon and Hill (2010) and Barrios-Miller and Siefferman (2013) found that parents preferentially care for brighter over duller male offspring. Because juvenile coloration influences parental feeding/defense decisions, our data suggest that the brightness of the blue-UV plumage of nestling male Eastern Bluebirds can function as an honest signal of quality.

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