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Structural and melanin coloration indicate parental effort and reproductive success in male eastern bluebirds

Lynn Siefferman and Geoffrey E. Hill
Department of Biological Sciences, 331 Funchess Hall, Auburn University, Auburn, AL 36830, USA

Male eastern bluebirds (*Sialia sialis*) have two types of ornamental plumage coloration: a brilliant blue-ultraviolet head, back, and wings, and a patch of chestnut breast feathers. The blue-UV coloration is produced from feather microstructure, whereas the chestnut coloration is produced by a combination of pheaomelanin and eumelanin pigments deposited in feathers. We tested the hypothesis that plumage coloration reflects male quality in eastern bluebirds, a socially monogamous, sexually dichromatic bird. We investigated whether male ornamentation correlates with mate quality and parental effort. We quantified three aspects of male ornament coloration: (1) size of the patch of chestnut breast feathers, (2) reflectance properties of the chestnut plumage coloration, and (3) reflectance properties of the blue-ultraviolet plumage coloration. We found that males with larger breast patches and brighter plumage provisioned nestlings more often, fledged heavier offspring, and paired with females that nested earlier. Males with plumage coloration that exhibit more ultraviolet hues fledged more offspring. These results suggest that plumage coloration is a reliable indicator of male mate quality and reproductive success. Both melanin-based and structural-based plumages appear to be honest signals of male quality and parental care that can be assessed by competitors or by potential mates. *Key words:* eastern bluebirds, parental investment, melanin color, plumage coloration, sexual selection, *Sialia sialis*, structural color. *[Behav Ecol 14:855–861 (2003)]*

The indicator model of sexual selection proposes that the expression of a sexually selected trait is correlated with individual condition. Because only exceptionally fit individuals in a population achieve maximum expression of such traits, these traits can act as honest signals of an individual's quality (Andersson, 1994; Hamilton and Zuk, 1982; Kodric-Brown and Brown, 1984; Zahavi, 1975). This model predicts that males who display more exaggerated traits compete better for mates and consequently experience higher reproductive success. Female choice for more ornamented males is adaptive if females benefit by choosing to mate with well-ornamented males. Such benefits could include higher rates of courtship provisioning, more help with parental care, better territory quality, better protection from predators, or good genes for offspring (Heywood, 1989; Hoelzer, 1989; Kirkpatrick and Ryan, 1991). Recent studies of birds have provided evidence that females can obtain benefits by choosing a mate based on the magnitude of his secondary sexual traits (Hasselquist et al., 1996; Hill, 1991, Moller and de Lope, 1994; Norris, 1990; Petrie, 1994).

Plumage coloration is among the most widespread and conspicuous of ornamental traits in birds. Ornamental plumage coloration can result from two primary mechanisms: pigments deposited in feathers and feather microstructure. Birds commonly use two types of pigments to color their plumage: melanins, which produce colors from chestnut to black; and carotenoids, which produce colors ranging from yellow to red. In addition, there are two types of melanin pigments: eumelanins, which are deposited in feathers as large, dark, regularly shaped granules and produce brown and black colors; and phaeomelanins, which are deposited in feathers as smaller, irregularly shaped granules and produce tan and chestnut coloration (Fox and Vevers, 1960; Gill, 1995). Structural coloration is fundamentally different from pigment-based plumage coloration because it is produced by microstructures in the reflective keratin of the feather. These keratin particles scatter longer wavelengths of light and reflect the shortest wavelengths, giving feathers a green, blue, purple, and iridescent coloration (Finger, 1995; Finger and Burkhardt, 1992; Fox, 1976). One type of structural plumage coloration that produces the noniridescent colors results from feather structures in the spongy, medullary layer of feather barbs (Prum et al., 1999). This layer is composed of a matrix of keratin rods and air vacuoles of varying shapes and sizes around a basal layer of melanin granules that surround a large, air-filled nuclear vacuole (Auber, 1957; Dyke, 1971). Because much of the structural color variation occurs in the ultraviolet range (300–400 nm), much of this variation is beyond human visual perception (Bennett et al., 1994). The visual system of most bird species, including all passerine birds tested to date, is sensitive to UV wavelengths (Chen et al., 1984).

Carotenoid- and melanin-based bird plumages often play an important role in conspecific interactions (Andersson, 1994). For instance, carotenoid-based colors have been shown in several species to act as honest signals to females of male quality (Hill, 2002), and eumelanin pigments often signal social dominance (see review by Senar, 1999). In a few species carotenoid displays signal dominance, and melanin color is used in mate choice (Moller, 1987a; Pryke et al., 2001). In contrast, the signaling functions of both structural and phaeomelanin plumage coloration have not been well studied. Recent studies of blue-black grassquits (*Guiraca caerulea*) and blue grosbeaks (*Volatinia jacarina*) suggest that structural plumage coloration is dependent on nutritional condition (Doucet, 2002; Keyser and Hill, 1999) and thus could reliably signal mate quality. Furthermore, in bluethroats (*Luscinia svecica*; Andersson and Amundson, 1997; Johnsen et al., 1998), European starlings (*Sturnus vulgaris*; Bennett et al., 1997), and blue tits (*Parus caerulies*; Andersson et al.,

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Address correspondence to L. Siefferman. E-mail: siefflm@auburn.edu.

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1998; Hunt et al., 1998, Sheldon et al., 1999) female choice for males with greater UV reflectance appears to favor structural plumage traits. The size of the phaeomelanin plumage ornament indicates male aggressiveness in yellow warblers (*Dendroica petechia*; Studd and Robertson, 1985) and nest initiation date in chestnut-sided warblers (*Dendroica pensylvanica*; King et al., 2001), suggesting that the extent of the chestnut ornament may be a sexually selected signal in these species.

Only one study has investigated the relationship between parental care and phaeomelanin coloration. Smiseth et al. (2001) found that the brightness of the phaeomelanin breast band of bluethroats was negatively related to paternal care. The two previous studies that have investigated the relationship between structural plumage coloration in males and potential benefits to mates found contrasting results. Keyser and Hill (2000) found positive associations between the intensity of structural coloration of male blue grosbeaks and both territory quality and chick provisioning rates, but Smiseth et al. (2001) found no relationship between any reflectance measure of the blue-UV plumage coloration of male bluethroats and parental care.

The aim of our study was to investigate whether male eastern bluebird ornamentation correlates with mate quality and reproductive success. Male eastern bluebirds have two types of ornamental coloration: a brilliant blue head, back, and wings and a chestnut breast patch. We quantified three color ornaments on males: (1) size of the chestnut melanin breast patch, (2) reflectance properties of the chestnut melanin plumage coloration, and (3) reflectance properties of the blue-UV structural plumage coloration. First, we investigated the relationship among these ornamental traits. Second, we investigated the relationship between male eastern bluebird ornamentation and his quality as a mate and reproductive success. We measured mate quality as the date that a male's mate laid her first egg, rate of incubation provisioning to females, and rate of male provisioning to offspring. We quantified chick quality as mean offspring mass at age 14 days, and seasonal reproductive success as the total number of offspring fledged. Finally, we quantified female provisioning rate to nestlings to determine whether female parental effort was correlated with her mate's ornamentation and whether her provisioning rates influenced the condition of the pair's offspring or their reproductive success.

METHODS

Study species

Eastern bluebirds are socially monogamous passerines that breed throughout eastern North America (Gowaty and Bridges, 1991). Bluebirds nest in cavities at the edge of open habitats and readily breed in nest-boxes. They are sexually dimorphic in plumage color: males exhibit bright blue-ultraviolet color over most of their back, head, wings, and tail, and chestnut coloration on their breast plumage. The blue-ultraviolet coloration is produced by feather microstructure, and the chestnut coloration is produced by both phaeomelanin and eumelanin pigments deposited in the feathers (McGraw K, unpublished data). Females are lighter in color with grayish-blue heads, backs, wings, and tail and smaller, lighter chestnut breast patches. In the southern United States, bluebirds breed from March to August, and pairs can produce three broods per year. The female constructs the nest, lays 3–6 eggs per nest, and incubates them for 12–14 days. Nestlings leave the nest cavity 16–22 days after hatching, but fledglings continue to rely on parental provisioning for another 2–3 weeks (Pinkowski, 1978). Bluebirds are primarily insectivorous. Males provide extensive parental care and feed females during egg laying and incubation (Kempenaers et al., 1998).

Population monitoring and marking

We conducted this study from March to August 1999 in Lee County, Alabama, USA. The 9-km^2 study site consisted of pastures and hay fields interspersed with small lakes, county roads, and fragments of hardwood forest. We captured males using an audio recording of an eastern bluebird song and a stuffed model to lure territorial males into mist nets. Females were trapped in nest-boxes while they brooded young nestlings. Each bird was individually marked with a unique combination of color bands and a U.S. Fish and Wildlife Service aluminum band. To avoid possible influence of color bands on mate choice, we did not use blue or purple bands (Burley et al., 1982; Johnsen et al., 1997).

We checked 75 nest-boxes at least once every 3 days throughout the breeding season. Nest-boxes with completed nests were monitored daily to document the date at which the first egg was laid. We calculated expected hatch date and monitored nests daily for hatching and fledging. When 14 days old, nestlings were banded and weighed to the nearest 0.05 g. The body weight of eastern bluebird nestlings increases sigmoidally until day 14 when the growth curve asymptotes at 90% of the adult value (Wittmann and Beason, 1992); thus nestling weight at day 14 is an approximation of fledgling weight. Reproductive success was calculated as the total number of putative offspring fledged by a pair over the course of the breeding season.

We recorded the rates that males provisioned incubating females and nestlings using Sony TRC 17 8mm video cameras. We placed video cameras 3 m from the nest-box for 4 h between 0600 and 1100 h. Nests were recorded on both the day 7 of incubation and on the day that chicks were 7 days old. Provisioning trips to nests were recorded as (1) number of feeding visits to female per hour, (2) number of male visits per hour per chick, and (3) number of female visits per hour per chick. As all pairs fledged at least two broods in the season, we used mean provisioning rates and mean offspring mass in our analyses.

Color analysis

Spectral data provide an objective way to quantify color (Cuthill et al., 1999; Endler, 1990). At time of capture, we collected the following feather samples from adult males for spectrometric plumage analysis: nine breast feathers, nine rump feathers, and the two outer tail feathers. Feathers samples were carefully plucked from the same location on all birds. The feathers were placed on black paper in a fashion that mimicked the way the feathers naturally lay on the bird. We stored the feathers in separate envelopes in a climate-controlled environment until spectrophotometric analyses were conducted. One researcher (L.S.) recorded spectral data with an Ocean Optics S2000 spectrometer (range 250–880 nm; Dunedin, Florida) using a micron fiber-optic probe at a 90° angle to the feather surface. Ambient light was excluded with a cylindrical metal sheath affixed to the probe tip, and the sheath was placed against the specimen with the probe held a fixed distance of 6 mm from the feather surface. The reading area was a 2-mm diameter of light illuminated with both a deuterium bulb (UV light source) and a tungsten-halogen bulb (visible light source). We generated reflectance data relative to a white standard (Labsphere, Inc.). Using OOIBase, a spectra acquisition software package, we recorded 20 spectra sequentially and then averaged the spectra to reduce electrical noise from the collection array within the spectrometer. This process was repeated five times, the probe lifted and replaced on the feather sample between each scan. We then averaged the five spectra for each body region for every male: the chestnut coloration from breast feathers and blue-UV coloration from the rump feathers and two outer tail feathers of each male. We quantified the blue-UV reflectance spectra by averaging the three blue-UV body regions sampled: rump and outer two tail feathers.

We quantified color using three standard descriptors of reflectance spectra: hue, chroma, and intensity of each individual. Hue refers to the wavelength at which the greatest amount of light is reflected. Chroma, a measure of spectral purity, is the ratio of the total reflectance in the range of interest and the total reflectance of the entire spectrum. Intensity is a measure of the brightness or amount of light reflected at the wavelength corresponding to hue; a high intensity is a bright color while a low intensity is a dark color. We calculated hue, chroma, and intensity differently for blue and chestnut plumage because of the inherent reflectance properties of the two colors. For structural coloration, we calculated hue as the wavelength at peak reflectance, chroma as the total blue-UV reflectance (300–500 nm) divided by the total reflectance (300–700 nm), and intensity as the amount (percentage) of light reflected at the peak wavelength (Figure 1). Because reflectance curves for the chestnut phaeomelanin coloration truncated at 700 nm, and all spectral curves were still increasing in reflectance at 700 nm, we calculated intensity as the amount (percentage) of light reflected at the wavelength of maximum slope and hue as the wavelength of maximum slope (Figure 1). We calculated chroma of chestnut coloration as the total orange-red reflectance (500–700 nm) divided by the total reflectance (300–700 nm; Figure 1).

To measure the size of the melanin-based breast patch of males, we placed a transparent plastic paper over the breast of each male and traced the outline of the breast patch. We scanned these outlines into a computer and used Sigma scan program to quantify patch area by pixel count.

Statistical analyses

We used two-tailed Pearson's correlations to explore the relationships among measures of male ornamentation. We found that extensive collinearity existed among our measures of ornamentation, thus we used principal components analysis to account for this interdependency. Because we made a priori predictions that plumage ornament elaboration should correlate positively with measures of mate quality, we used one-tailed Pearson's correlations to test the relationships between measures of ornamentation and first egg date, male provisioning rates, offspring mass, and reproductive success. Our two independent measures of plumage ornamentation increase the likelihood of significance arising by chance, so we applied sequential Bonferroni corrections to reduce the α level from 0.05 to 0.025 (Sokal and Rolf, 1995). Furthermore, in some cases, we used post-hoc partial correlations to clarify relationships between ornamentation and reproductive success. We used two-tailed Pearson's correlations to examine the relationship between male ornamentation and female provisioning rates as well as the relationships between female provisioning rates and offspring quality and reproductive success because we did not have a priori predictions. Data were transformed because they were not normally distributed. We used log transformation for chick mass, first egg date, intensity, hue, and patch size. We used log plus one transformation for reproductive success and arcsin transformation for chroma and provisioning rates.

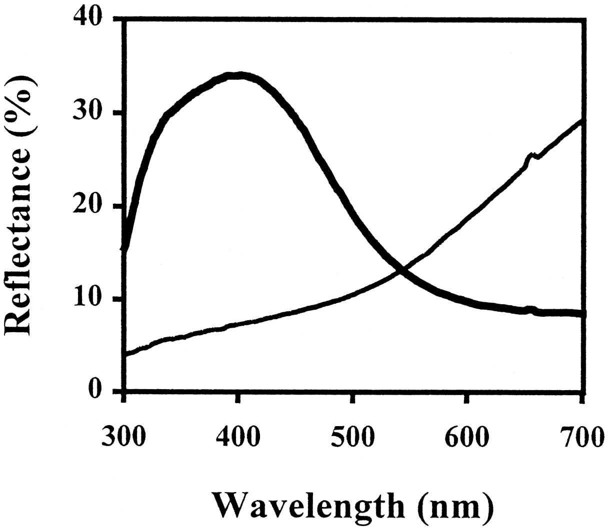

Figure 1
Reflectance spectrum of structural plumage (thick line): hue is the wavelength of maximum reflectance; chroma is the proportion of blue-UV reflectance to the total reflectance ($R_{300-500}/R_{300-700}$); and intensity is amount of light (percent reflectance) at hue wavelength. For melanin plumage (thin line); hue is wavelength of maximum slope; chroma is the proportion of orange-red reflectance to the total reflectance ($R_{600-700}/R_{300-700}$), and intensity is the amount of light (% reflectance) at the maximum.

RESULTS

Relationships among multiple measures of male ornamentation

We found significant interdependency among plumage ornaments of male eastern bluebirds (Table 1). First, males exhibiting higher chroma of structural plumage coloration (more spectrally pure) tended to exhibit more intense structural plumage coloration (percent light reflected at peak wavelength). Males exhibiting higher chroma of structural plumage coloration also tended to exhibit more ultraviolet hue. We made two principal components because intensity and chroma correlated strongly with the first principal component, whereas hue and chroma correlated strongly with the second principal component (Table 2). Second, there were significant relationships among the reflectance descriptors of chestnut coloration and chestnut patch size. Males with lower intensity (darker) chestnut coloration tended to have larger patch sizes. The chroma of the chestnut coloration was inversely related to chestnut intensity, such that males exhibiting purer chestnut coloration exhibited darker coloration. All measures of chestnut ornamentation loaded heavily on the first principal component of male ornamentation. Third, the chestnut ornamentation and reflectance measures of blue-UV chroma were associated, such that males with larger melanin breast patches exhibited more spectrally pure structural plumage.

To recapitulate, the patch size, reflectance measures of chestnut coloration, and brightness of the blue-UV coloration contributed to the first principal component of male ornamentation, whose eigenvalue explained 37% of the variation in male plumage ornamentation. The hue and chroma of the blue coloration contributed strongly to the second principal component of male ornamentation, explaining 22% of the variation in male plumage ornamentation. Thus, males with higher values of the first principal component displayed larger chestnut breast patches, darker chestnut coloration, and brighter blue coloration (Table 2). Also, males with

Table 1

Results from a two-tailed Pearson correlation matrix among multiple measures of male eastern bluebird ornamentation

	Chestnut plumage				Blue plumage	
	Size	Intensity	Chroma	Hue	Intensity	Chroma
Chestnut plumage						
Intensity	−.51** (28)					
Chroma	.29 (28)	−.38* (36)				
Hue	−.19 (28)	.29 (36)	−.24 (36)			
Blue plumage						
Intensity	.23 (25)	−.32 (27)	.14 (27)	.29 (27)		
Chroma	.44* (25)	−.36 (27)	.15 (27)	−.24 (27)	.55** (29)	
Hue	−.04 (25)	−.16 (27)	.15 (27)	−.15 (27)	.07 (29)	−.45** (29)

Ornamentation includes both chestnut patch size and coloration (intensity, chroma, and hue) and blue-UV coloration (intensity, chroma, and hue). Values given are correlation coefficients. Numbers in parentheses are n.

* $p \le .05$; ** $p \le .01$.

higher values of the second principal component displayed spectral peaks that were shifted to the most extreme ultraviolet coloration (hue) and purer blue-UV coloration (Table 2).

Ornamentation and first egg date

The first principal component of male ornamentation was negatively associated with the date at which its mate laid her first egg. This indicates that males with larger breast patches and greater intensity of blue-UV coloration paired with females who nested earlier (Table 3, Figure 2).

Ornamentation and provisioning rates

We found no relationships between measures of ornamentation and male provisioning to mates during incubation (Table 3). Also, we did not find an association between either the first principal component of male ornamentation and female provisioning rates to nestlings ($r = .14$, $n = 15$, $p = .62$), nor between the second principal component of male ornamentation and female provisioning rates to nestlings ($r = .004$, $n = 15$, $p = .99$). Thus, females do not appear to adjust their parental effort in relation to the attractiveness of their mates.

The first principal component of male ornamentation was positively correlated with the rate at which males provisioned nestlings, such that males with larger, darker breast patches and greater intensity of blue-UV coloration fed nestlings more often (Table 3, Figure 3), however the relationship was not significant after the sequential Bonferroni adjustment.

Table 2

Eigenvectors for the first and second principal component (PC1 and PC2) of a principal component analysis on seven color characteristics for male eastern bluebirds

Ornament	Component 1	Component 2
Chestnut patch size	0.734	0.085
Chestnut intensity	−0.768	0.281
Chestnut chroma	0.651	−0.361
Chestnut hue	−0.543	0.395
Blue intensity	0.593	0.312
Blue chroma	0.656	0.672
Blue hue	0.029	−0.813

Ornamentation, nestling weight, and reproductive success

The first principal component of male ornamentation was positively correlated with fledgling mass, indicating that males with larger breast patches and brighter blue-UV coloration raised heavier offspring (Table 3, Figure 4). Because provisioning rates may affect the mass of offspring, we used post hoc partial correlations to test whether the first principal component of male ornamentation was significantly related to fledgling mass if we removed the effect of paternal provisioning. The relationship between male ornamentation and offspring mass was stronger when the effect of provisioning was removed ($r = .49$, $n = 11$, $p = .04$); however, the relationship was not significant after the sequential Bonferroni adjustment. Furthermore, we found no significant relationship between female provisioning rates to nestlings and nestling weight ($r = .20$, $n = 24$, $p = .34$).

The second principal component of male ornamentation was positively correlated with the reproductive success of the pair such that males with more UV and more spectrally pure blue-UV plumage fledged more offspring (Table 3, Figure 5). Because the first egg date and provisioning rates might be associated with the pair's reproductive success, we used post hoc partial correlations to investigate whether the first principal component of male ornamentation was significantly related to reproductive success after we removed the effects of the first egg date and paternal provisioning rate. The relationship between male ornamentation and the number of offspring fledged was significantly associated ($r = .66$, $n = 17$, $p < .01$). Furthermore, we found no significant relationships between female provisioning rates to nestlings and the pair's reproductive success ($r = .05$, $n = 22$, $p = .82$).

DISCUSSION

We found that more ornamentation in males, characterized by larger, darker chestnut patches and brighter blue-UV coloration, is correlated with paternal investment and offspring condition. Our data are consistent with Smiseth's et al.'s (2001) and Keyser and Hill's (2000) studies indicating that chestnut coloration in bluethroats and blue coloration in blue grosbeaks predict parental provisioning rates. Nestling mass at fledging is known to influence subsequent survival in passerines, with heavier offspring surviving better (Perrins, 1965). The relationship between male ornamentation (patch size and coloration brightness) and chick mass at fledging

Table 3

Results from a one-tailed Pearson correlation between measures of male ornamentation and his mate's first egg date, nestling mass, and female reproductive success

Ornamentation	First egg date ($n = 23$)	Incubation provisioning rate ($n = 21$)	Nestling provisioning rate ($n = 15$)	Offspring mass ($n = 18$)	Reproductive success ($n = 20$)
Principal component 1	−.46***	−.15	.44*	.46**	.10
Principal component 2	.15	.05	−.28	−.10	.62***

PC1 of a principal components analysis of male ornamentation is composed primarily of chestnut patch size and coloration (intensity and chroma) and blue coloration (intensity and chroma). PC2 of a principal components analysis of male ornamentation is composed primarily of hue and chroma of blue-UV coloration. First egg date is measured as Julian day of year, incubation provisioning is number of provisioning per minute, nestling provisioning rate is number of provisions per nestling per minute, nestling mass is a brood mean on nestling age 14 days, and reproductive success is total number of fledged offspring for all broods in 1999. Values are correlation coefficients.

* $p \leq .05$; ** $p \leq .025$; *** $p \leq .01$.

indicates that offspring of more ornamented males are in better condition and thus more likely to survive.

In contrast to this association between patch size and plumage brightness and parental care, we found that more ultraviolet (spectral peak shifted to the left) and more pure blue-UV coloration were correlated with reproductive success such that males with a more ultraviolet hue produced more offspring. We found no evidence for a relationship between hue of structural coloration and measures of parental care. These observations suggest that different components of the plumage coloration of male eastern bluebirds may indicate two different aspects of male quality (Badyaev et al., 2001). The brightness of blue and chestnut color and size of the chestnut patch may signal a male's potential to provide resource benefits to females, while the ultraviolet hue of the structural coloration may signal male genetic quality. Offspring may be more likely to survive to fledging if they inherit good genes from their fathers. The suggestion that the hue and chroma of male eastern bluebird structural coloration signals good genes is supported by evidence that variation in the blue-UV crown of male blue tits indicates their genetic quality (Sheldon et al., 1999). Our study documents for the first time a relationship between structural plumage color and reproductive success, measured in terms of number of offspring fledged per year.

A third possible attribute signaled by male plumage coloration is the quality of resources a male can provide. We found that melanin breast-patch size and reflectance measures of chestnut and blue-UV coloration were strongly positively associated with first egg date. First egg date could indicate either male competitive ability for access to breeding territories or female preference if females of early-mated males start egg laying earlier (Alatalo et al., 1984). The size of the eastern bluebird's breast patch, which is a mixture of both phaeomelanin and eumelanin pigments, may signal male competitive ability in the same manner that eumelanin badge

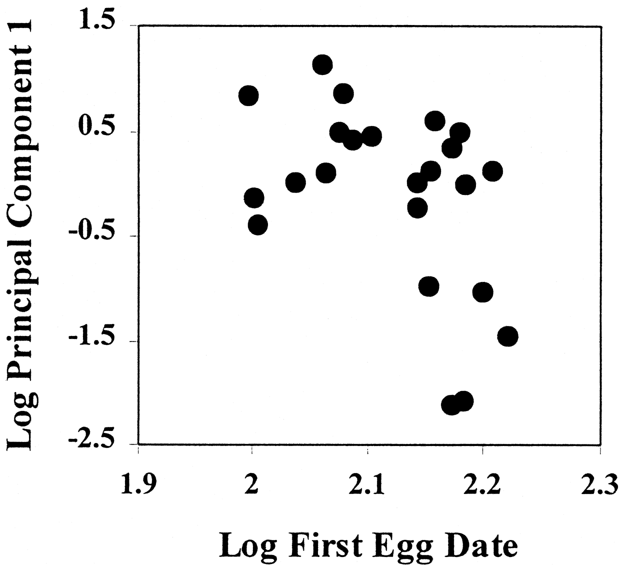

Figure 2
The relationship between female's first egg date (log) and the first principal component of male coloration ($r = -.46$, $n = 23$, $p = .01$). PC1 of a principal component analysis of male ornamentation is composed primarily of chestnut patch size and coloration (intensity and chroma) and blue coloration (intensity and chroma).

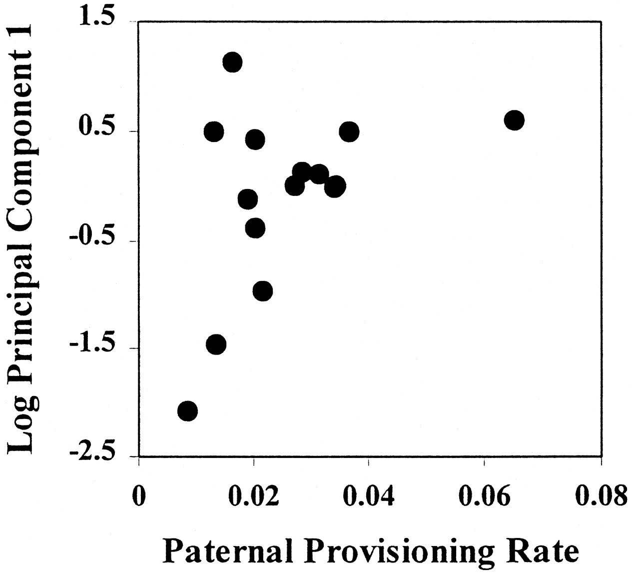

Figure 3
The relationship between male provisioning rates to nestlings (number of provisions/chick/minute; arcsin) and the first principal component of male ornamentation ($r = 0.44$, $n = 15$, $p = .05$). PC1 of a principal component analysis of male ornamentation is composed primarily of chestnut patch size and coloration (intensity and chroma) and blue coloration (intensity and chroma).

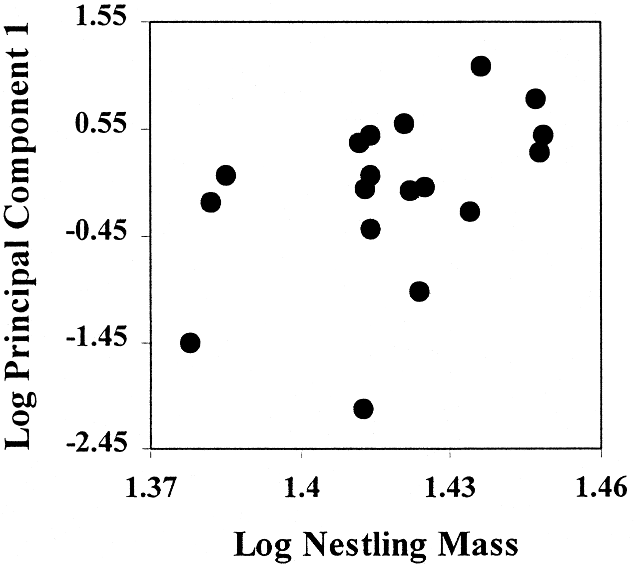

Figure 4
The relationship between mean nestlings weight (g) at day 14 (asymptotic weight; log) and the first principal component of male ornamentation ($r = .46$, $n = 18$, $p = .02$). PC1 of a principal component analysis of male ornamentation is composed primarily of chestnut patch size and coloration (intensity and chroma) and blue coloration (intensity and chroma).

size has been shown to reliably act as a "badge of status" in house sparrow; mediating male–male competition for nest sites (Moller, 1987b).

If both melanin ornamentation and structural plumage coloration are condition-dependent traits that relate to some aspect of quality, then they should both be affected by environmental variables. Until recently, the potential function of structural plumages as honest signals of male quality was dismissed because of the lack of evidence of costs associated with production of such traits (Gray, 1996). However, recent studies indicate that the production of structural plumage coloration is affected by nutritional condition (Doucet, 2002; Keyser and Hill, 1999). Eumelanin coloration seems to be less sensitive to poor nutritional condition and parasites than does carotenoid coloration (Hill and Brawner, 1998; McGraw and Hill, 2000), but stress induced by brood manipulation alters the eumelanin ornaments of both parents and offspring in house sparrows (Griffith et al., 1999). The expression of both structural and melanin coloration in bluebirds may both be affected by similar factors, making them reliable indicators of condition. Controlled experiments that test the production and maintenance costs of structural and phaeomelanin coloration are needed to better understand the information content of eastern bluebird coloration.

In conclusion, we found support for the hypothesis that females mated to more colorful males receive benefits from their mates. Our observations indicate that male eastern bluebirds vary in their plumage ornamentation. Plumage ornamentation is correlated with parental care, chick quality, and reproductive success, so females could use expression of these traits to identify high-quality partners. The mechanism of sexual selection remains to be tested. The relationship between ornamentation, paternal provisioning, and reproductive success indicate that females could benefit by choosing mates based on their plumage coloration. Trends between the ornamentation and first egg date suggest that males use ornamentation to mediate competitive interactions over nest sites. For eastern bluebirds or virtually any species of bird, however, we have yet to conduct experimental tests to determine whether phaeomelanin and structural plumages are condition-dependent traits. Ultimately, experiments will be needed to deduce to what degree plumage ornamentation in eastern bluebirds function in female choice versus male–male competitive interactions.

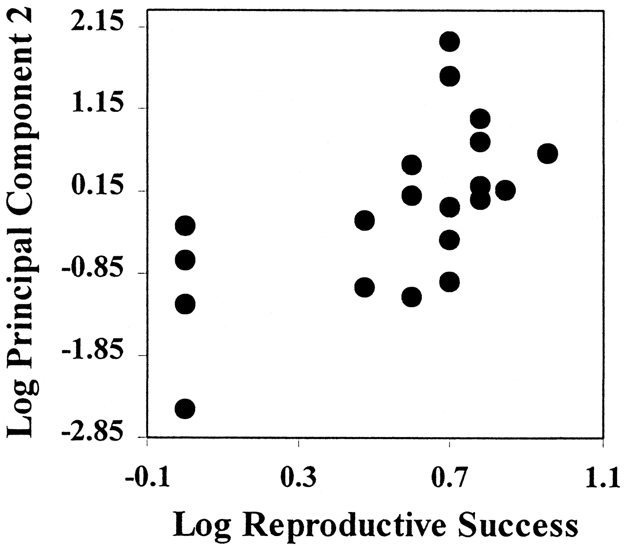

Figure 5
The relationship between reproductive success (number of offspring fledged in the season; log plus 1) and the second principal component of male ornamentation ($r = .62$, $n = 20$, $p = .002$). PC2 of a principal component analysis of male ornamentation is composed primarily of hue and chroma of blue coloration.

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