
Blue Structural Coloration of Male Eastern Bluebirds Sialia sialis Predicts Incubation Provisioning to Females

Author(s): Lynn Siefferman and Geoffrey E. Hill

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Lynn Siefferman and Geoffrey E. Hill

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Plumage coloration has been suggested to serve as an honest signal of benefits that males provide to females. One benefit proposed for females that choose to mate with elaborately colored males is that such males might provide more food resources to the females. To test this hypothesis, we investigated the relationship between the rates at which males provisioned incubating females and the structural ultraviolet (UV)/blue coloration and melanin-based chestnut coloration of male eastern bluebirds *Sialia sialis*, a sexually dichromatic songbird in which coloration has been shown to be sexually selected in males. We found that males with brighter UV/blue coloration provisioned incubating females more often than did drabber males. Melanin coloration, however, was not correlated with provisioning rates. Moreover, provisioning rates were correlated with the length of time that females spent off the nest, indicating an important benefit of increased male provisioning. These data support the hypothesis that female bluebirds receive direct resource benefits by pairing with males with bright structural coloration.

L. Siefferman (correspondence) and G. E. Hill, Department of Biological Sciences, 331 Funchess Hall, Auburn University, Alabama, USA 3684. E-mail: siefflm@auburn.edu

In birds there is considerable variation in male parental roles during incubation. In some species, females are totally dependent on males for food during the incubation stage (e.g. hornbills, family Bucerotidae, Lack 1968), but it is more common for incubating females to receive some food from their mates and to acquire the remainder through their own foraging (Williams 1966, Ligon 1999). Food provided by males during incubation has been proposed to be an important energy source for females (Niebuhr 1981). Indeed, several studies have demonstrated that males that provide higher rates of incubation feeding to mates can improve female body condition and reduce the time she spends foraging for herself (e.g. Lyon and Montgomerie 1985, Lifjeld and Slagsvold 1986, Halupka 1994). Incubation feeding could thus increase reproductive output because time off the nest during incubation can influence the mortality rates or the development rate of embryos (White and Kinney 1974, Nilsson and Smith 1988). These observations suggest that females would benefit if they paired with males that are better than average at providing food during incubation.

The plumage coloration of males has been proposed to serve as a signal of male foraging ability and hence the ability of a male to provide food during incubation (Hill 1991). Indicator models of sexual selection propose that sexually selected traits like ornamental plumage coloration signal information to potential mates (Zahavi 1975, Kodric-Brown and Brown 1984, Andersson 1994). Plumage color is most commonly derived from one of three distinct mechanisms: carotenoid pigments, melanin pigments, or feather microstructure (Fox and Vevers 1960, Hill and McGraw 2006). Colors that result from these different mechanisms may have different costs associated with their production, and hence signal different information to females (Hill 2006). There is growing evidence that full expression of structural coloration requires excellent nutrition through the molt period while melanin coloration appears to be less sensitive to food deprivation (McGraw et al. 2002, Siefferman and Hill 2005a). Thus the expression of structural coloration may be a signal of foraging ability. One important benefit to females is the males' ability to procure food resources. If foraging ability during the period of feather growth is a good predictor of foraging ability during the breeding period, then females could use expression of structural coloration to predict the resource contribution of potential mates.

Most studies that have quantified male provisioning rates in relation to male ornamentation have focused on nestling rearing (e.g. Smiseth et al. 2001), with the assumption that provisioning during incubation is less demanding for the male and of less benefit to the female (Stearns 1992, Monaghan and Nager 1997). Thus, even though incubation feeding by males has been proposed to affect female reproductive success and fitness, few studies have addressed whether sexually selected traits act as honest indicators of the amount of provisioning that males bring to their mates during the incubation stage (but see Hill 1991, Siefferman and Hill 2003).

Here we study incubation feeding in relation to the plumage coloration of male eastern bluebirds *Sialia sialis*. Eastern bluebirds are sexually-dichromatic, obligate cavity-nesting passerines. Only females incubate eggs, but males feed females during the pairing and incubation stages and both sexes care for young. Males exhibit brilliant UV-blue, structurally-based plumage coloration over their back, head, wings, and tail, and chestnut melanin-based plumage coloration on their breast. A study that combined structural and melanin plumage coloration into a composite plumage score using principal components analysis found that more colorful males (brighter structural coloration and darker melanin coloration) provisioning offspring more often and mated earlier in the season, but found no relationship between the composite color score and incubation provisioning rates (Siefferman and Hill 2003). More recent research demonstrates that structural coloration, but not melanin coloration, in this species is linked to nutritional condition during the molt period in females (Siefferman and Hill 2005a) and structural coloration of males is positively related body condition, age, and the ability to gain access to limited nest sites (Siefferman et al. 2005, Siefferman and Hill 2005b). These observations suggested that structural plumage coloration could be a reliable indicator of foraging ability in bluebirds and that we may have obscured patterns of male provisioning and structural coloration by combining structural and melanin-based coloration in our study (Siefferman and Hill 2003). In another year, we again tested the hypothesis that ornamental coloration is a signal of male provisioning in the eastern bluebird. We measured plumage coloration from the same patches on the bird, but this time we kept separate our analyses of the relationships between number of feeding visits to incubating females and the structural blue and melanin chestnut coloration of provisioning males. Additionally, to determine whether incubation provisioning affects the energy budgets of females, we assessed whether provisioning during incubation influences the time that females spend foraging during the incubation stage. Finally, we investigated whether provisioning rates during incubation influenced the length of the incubation period and hatching success.

Methods

We studied a marked population of eastern bluebirds in Lee County, Alabama between March and August 2001. Nest boxes were monitored throughout the breeding season to determine the number of eggs and chicks in each nest and length of the incubation period. We captured birds at nest sites in early spring and marked them with unique combinations of three color bands and one numbered metal band. We estimated the age of all newly banded birds as either 2nd-year (nestlings during the prior spring/summer) or after-2nd-year (older) based on the shape of the 10th primary feather (Pitts 1985).

We measured the rates at which males provisioned females using 8 mm video cameras mounted to tripods at a distance of 3 m from the nest. We recorded activity at the nest for 4 continuous hrs beginning between 0600 and 0700, on the seventh day of incubation. During a nest watch, we recorded the times an incubating female entered and left the nest as well as visits by males to feed females. The mate of the incubating female usually came into the nest cavity with food. Occasionally, a male would call to his mate from just outside of the nest box and the female would leave to collect food from the male. If a female stayed outside of the nest cavity for less than 30s this time was not subtracted from the period of nest attendance and the period was classified as a single incubation bout. When males provisioned females just outside of the nest box we considered it to be an incubation feeding.

Upon capture, we collected samples of 9 blue rump feathers, 2 blue outer tail feathers, and 9 chestnut breast feathers from each male for spectrometric plumage analysis. We took reflectance measurements with an Ocean Optics S2000 spectrometer (range 250–880 nm: Dunedin, FL, USA) using a bi-furcated micron fiber optic probe at a 90° angle 5 mm from the feather surface. This 2-mm measurement area was illuminated with both UV (deuterium bulb) and a visible (tungsten-halogen bulb) light sources. Reflectance data were generated relative to a white standard (Labsphere, Inc.). We recorded and averaged 20 spectra sequentially and then recorded five randomly chosen points on each sample using OOIbase software (see Andersson and Prager 2006 for more details on spectral analysis of feathers). Using spectral processing program (ColouR v1.7, Queens, Ontario), we summarized reflectance data by calculating three standard descriptors of reflectance spectra: brightness, chroma, and hue (following protocols of Siefferman et al. 2005). Brightness, or total amount to light reflected by the feather, is the summed reflectance from 300 to 700 nm. Chroma and hue were calculated differently for UV-blue and chestnut coloration because of the inherent reflective properties of the two colors. For the rump and tail feathers, UV chroma, a measure of spectral purity, was calculated as the ratio of the UV reflectance (300–400 nm) to the total reflectance (300–700 nm). For the chestnut breast feathers, red chroma was calculated as the ratio of the total reflectance in the red range (575–700 nm) to the total reflectance of the entire spectrum (300–700 nm). Hue is the principal color reflected by the feather. For structural coloration (rump and tail) hue was calculated as the wavelength at peak reflectance. Because hue (calculated as maximum slope) of the chestnut breast feathers expressed very little variation among males, we do not report hue for breast coloration. Because rump and tail coloration are both derived from structural reflectance and are correlated (Siefferman et al. 2005), we averaged the scores from these body regions. This methodology differs from that of the past (Siefferman and Hill 2003) that employed principal components analysis to combine both structural and melanin plumage. Here, we analyze structural and melanin coloration separately because nutritional stress experiments (Siefferman and Hill 2005a) and correlations between age, body condition, and coloration (Siefferman et al. 2005) suggest that structural and melanin plumage traits may signal fundamentally different information.

Results

To determine the value of structural and melanin plumage color in predicting incubation provisioning rates, we constructed a backward stepwise multiple regression model. In this model, we included structural (brightness, UV chroma, and hue) and melanin (brightness and red chroma) color scores as potential predictor variables. Two significant models emerged from this analysis. The model with the most predictive power included both structural brightness and UV chroma ($R^2 = 0.26$, $F^2_{25} = 4.5$, $P = 0.02$), such that males that displayed brighter coloration and displayed greater UV chroma fed incubating females most often. The second and most parsimonious model included only brightness of structural plumage coloration as a significant predictor of incubation provisioning (Fig. 1), suggesting that brightness is the best predictor of provisioning behavior. No aspect of melanin-based breast coloration was significantly related to incubation provisioning in any model.

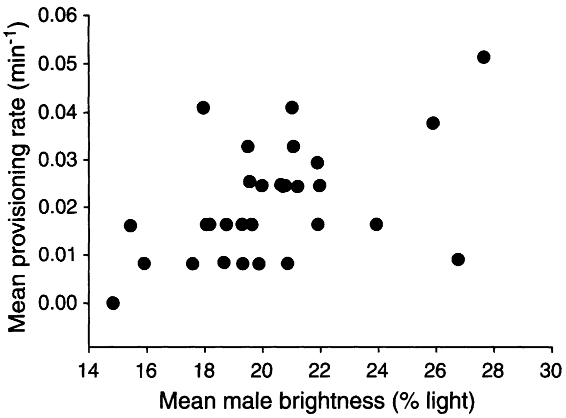

Fig. 1. Relationship between male provisioning rates to incubating females (number of provisions/minute) and the brightness of the structural plumage of male eastern bluebirds ($R^2 = 0.23$, $F^1_{26} = 7.6$, $P = 0.01$).

Because seasonality could influence plumage coloration via feather wear, we used correlations to test whether the brightness of structural plumage coloration was significantly related to date of capture. There was no significant relationship between male brightness and capture date ($r = 0.07$, $n = 28$, $P = 0.73$). Moreover, male age did not significantly influence feeding rates as there was no difference between feeding rates of after-2nd-year (0.02 feeding $\mathrm{min}^{-1} \pm 0.01$) and 2nd-year males (0.02 feeding $\mathrm{min}^{-1} \pm 0.02$; $t = -0.14$, $n = 23,7$, $P = 0.89$).

The length of time that females spent away from the nest was significantly negatively related to how often she was fed by her mate (Fig. 2), indicating that females that

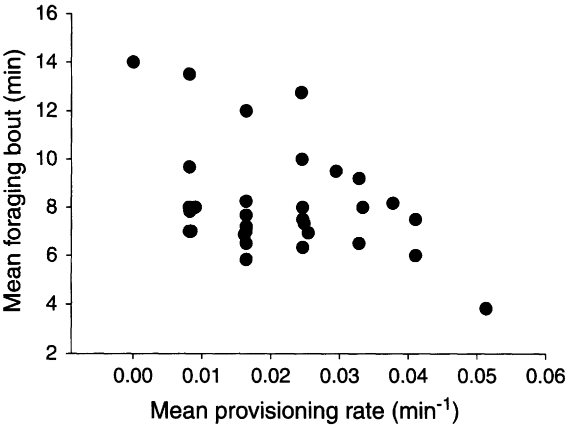

Fig. 2. Relationship between male provisioning rates to incubating female eastern bluebirds (number of provisions/minute) and the average number of minutes that females spent off the nest during the incubation stage ($r = -0.38$, $n = 32$, $P = 0.03$).

were fed more often spent less time foraging on their own. We found no significant relationships between male provisioning rates during incubation and hatching success ($r = -0.04$, $n = 32$, $P = 0.84$) or length of incubation period ($r = 0.13$, $n = 27$, $P = 0.51$).

Discussion

We found that male eastern bluebirds with brighter structural plumage coloration provisioned their mates more often during the incubation stage than did duller males. The positive relationship between structural plumage ornamentation of males and food delivery to females indicates that females could use expression of this trait to identify partners that will provision well during incubation. Although much research has focused on whether male coloration can act as an honest signal of parental provisioning rates to offspring, incubation provisioning has rarely been addressed (but see Hill 1991, Siefferman and Hill 2003). In fact, although incubation has been demonstrated to be energetically expensive (Vleck 1981), incubation is too often ignored in estimates of the cost of reproduction in life-history studies (reviewed in Monaghan and Nager 1997, Reid et al. 2002).

Here, we assessed plumage ornamentation of the structurally- and melanin-based feathers separately because the UV-blue coloration of the rump and tail is produced by the feather nanostructure (Shawkey et al. 2003) while the chestnut coloration of the breast is caused by the deposition of melanin pigments (McGraw et al. 2004). This analysis differs from that of our previous attempt to test the relationship between incubation provisioning and plumage coloration (Siefferman and Hill 2003) because in our earlier study we used Principal Components Analyses (PCA) to create composite variable of structural and melanin coloration of breast, rump, and tail. PCA has the advantage of collapsing interrelated plumage characteristics (Siefferman et al. 2005) and facilitates the reduction the number of color variables (Montgomerie 2006). Subsequent research with this species (Siefferman and Hill 2005a) and in brown-headed cowbirds *Molothrus ater* (McGraw et al. 2002), however, indicates that structural coloration but not melanin coloration is influenced by nutritional stress, suggesting that these plumages could signal fundamentally different information. While some authors have proposed that different ornamental traits should be positively correlated (Kodric-Brown and Brown 1984), others have hypothesized that different ornaments might signal fundamentally different things about an individual (Møller and Pomiankowski 1993, Andersson et al. 2002). With plumage data collected from the same study population but in a different year than the current study, we found that a composite variable of structural and melanin coloration was not significantly related to male incubation provisioning (Siefferman and Hill 2003). Here we found that the brightness and chroma of structural coloration was positively related to incubation provisioning but that no aspect of melanin coloration showed any significant relationship with incubation feeding. These observations underscore the importance of statistical methodology in assessing multiple traits.

UV-blue plumage coloration in male eastern bluebirds appears to be a costly trait that is maintained via sexual selection. Males aggressively compete for access to nest boxes and previous work with this population demonstrated that more ornamented males (greater UV chroma and brighter) are better able to compete for access to nest cavities than duller males (Siefferman and Hill 2005b). Non-iridescent blue structural coloration in birds is produced as a function of the size and arrangement of nanostructural elements within the medullary layer of feather barbs (Prum et al. 1998, Prum 2006). The feathers of eastern bluebirds are composed of a spongy medullary layer within the feather barbs lying beneath a keratin cortex and above a layer of melanin granules surrounding large, central vacuoles (Shawkey et al. 2003). Transmission electron microscopy of feathers demonstrates that variation in coloration is determined by feather structure; brighter feathers have a thinner cortex surrounding the medullary layer while feathers with greater UV chroma have shorter distances between the scattering elements (i.e., keratin rods and air spaces; Shawkey et al. 2003, 2005). The precision of this nanostructural arrangement suggests that physiological condition during molt can influence the ability to produce optimal feather nanostructure. Indeed, previous work with this population demonstrated that structural coloration is influenced by manipulations of reproductive effort prior to molt (Siefferman and Hill 2005c) and by nutritional stress during molt (Siefferman and Hill 2005a).

An alternative explanation for the relationship between structural plumage coloration and provisioning rates is that males that provision more experience greater feather wear. The reflectance measures of structural plumage in blue tits vary with season, and it has been suggested that feather wear or the accumulation of dirt on the feather creates this seasonal trend (Örnborg et al. 2002). Blue tits measured soon after molt exhibited hues shifted more towards the UV, greater UV chroma, and lower brightness than birds measured several months later in the year. If the brightness of eastern bluebirds was affected by time since feather growth in the same manner as in the blue tits, then seasonal changes in brightness and provisioning rate could have created the patterns that we report in this paper. However, there was no significant relationship between brightness and capture date. Capture date was probably not related to plumage color in our population because all captures were completed within one month. Age could also influence the ability of eastern bluebirds to provision mates and older male bluebirds do tend to be brighter and in better body condition than younger males (Siefferman et al. 2005). We found no difference, however, in the provisioning rates of older and younger males.

We found that females paired to males that provision well spent less time foraging, suggesting that incubation feeding influenced the energy budgets of incubating female bluebirds. Our data are consistent with studies of other passerine birds that demonstrate food availability (Moreno 1989) and incubation provisioning rates (Radford 2004) influence nest attendance. It has been suggested that increased nest attendance decreases the length of incubation period and/or increases hatching success (reviewed in Webb 1987). In this way, male bluebirds could increase their breeding success by provisioning females during courtship and incubation. Although female bluebirds that were well provisioned spent less time away from their nests, we found no evidence that male provisioning during incubation influenced the hatching success or length of the incubation period. Female bluebirds may behave so as to insure that their eggs hatch within a normal period, allowing their own body condition to decline when not fed adequately during incubation.

Another potential benefit of mating with a male that provisions well during the egg laying and incubation periods is that such male behavior could enable females to guard their boxes more diligently. Bluebirds are obligate secondary cavity nesters and both males and females compete vigorously against same-sex conspecifics for nest sites (Gowaty and Wagner 1988). Removal experiments have shown that females from this population are usually replaced within 24 hr of departure from their territory, indicating the existence of a large number of unmated females (authors unpubl. data). Moreover, in this species, conspecific brood parasitism occurs (up to 10% of offspring, Gowaty and Karlin 1984). Female bluebirds guard their boxes against conspecific females that may either attempt to dump eggs or usurp nest sites (Gowaty 1981, Gowaty et al. 1989). Thus, it seems reasonable that females that are able to spend more time at their nest boxes will be better able to guard their nests.

In conclusion, we found support for the hypothesis that females mated to brighter UV-blue males receive direct resource benefits during incubation, suggesting that females could use structural plumage to identify high quality partners. Males displaying brighter structural coloration males may forage more efficiently or may allocate a greater amount of energy toward feeding mates. Alternatively brighter males may provision females more often because they have access to higher quality territories. Ultimately, experiments are needed to disentangle the effects of territory quality and superior foraging ability on male provisioning rates.

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