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Parental Investment and Male Ornamentation in the Eastern Bluebird (*Sialis Sialis*)

Daniel Paul Wetzel

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PARENTAL INVESTMENT AND MALE ORNAMENTATION IN THE EASTERN
BLUEBIRD (*SIALIA SIALIS*)

by

DANIEL P. WETZEL

(Under the Direction of C. Ray Chandler)

ABSTRACT

Bright plumage coloration in most birds is thought to be a product of sexual selection. Brighter, more-ornamented males are preferred by females because their plumage conveys information regarding the quality of the individual. One measure of male quality is willingness to invest in offspring. In birds, investment is usually measured as the rate at which nestlings are provisioned. However there are other forms of parental investment. The purpose of this study is to quantify the relationship between two measures of parental investment and their association with structural plumage coloration in male Eastern Bluebirds (*Sialia sialis*). I found there was no correlation between nestling provisioning and nest defense for males or females. Males with brighter UV-blue plumage tend to provision nestlings at higher rates and more-ornamented males tend to defend the nest from a predator at lower rates. This study suggests that structural coloration is an indicator of the ability of a male to invest in its young. However, because nestling provisioning and nest defense (the two main male parental investments) were not correlated, I suggest that nestling provisioning and nest defense are not equivalent measures of parental investment, and condition-dependent traits have different relationships to different measures of parental investment.

INDEX WORDS: Parental investment, Sexual selection, Structural coloration, Nest defense, Eastern Bluebird, *Sialia sialis*

PARENTAL INVESTMENT AND MALE ORNAMENTATION IN THE EASTERN
BLUEBIRD (*SIALIA SIALIS*)

by

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Bachelor of Science, Illinois Wesleyan University, 2004

A Thesis Submitted to the Graduate Faculty of Georgia Southern University in Partial
Fulfillment of the Requirements for the Degree

MASTER OF SCIENCE

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INTRODUCTION

Sexual selection arises from differences in reproductive success, which are created by advantages certain individuals have over others of the same sex in regards to reproduction (Darwin 1871). Sexual selection can act in two ways: through direct competition for mates, intrasexual selection, or through mate-choice, intersexual selection. Intrasexual selection acts when members of the same sex, typically males, compete among themselves for the opportunity to access individuals of the opposite sex. When intrasexual selection occurs in a species, we usually observe males with weaponry such as large horns, antlers, or spurs (Darwin 1871, Fisher 1930). Intersexual selection, however, is driven by mate-choice; therefore one sex must be able to choose a mate based upon a conspicuous trait such as bright color, enlarged fins, elaborate songs, or enhanced scent (Darwin 1871, Fisher 1930, Andersson 1994). Natural selection favors those organisms that are best suited for their environment, whereas sexual selection favors organisms that can out-compete rivals for mates, or possess certain traits that make them attractive to mates. Thus, traits favored by sexual selection may be selected against by natural selection.

There have been several theories proposed that address how ornaments, such as bright plumage color in birds, can evolve even though they are not favored by natural selection. Darwin (1871) first suggested that females develop a preference for a trait in males. Females then act as a selecting agent, only mating with those individuals that possess the trait. Although Darwin had no evidence, he suggested that sons of selected individuals will inherit the preferred trait, and daughters will inherit a preference for that trait. Fisher (1930) expanded this idea and developed the "runaway model" of sexual

selection. Fisher suggested that the evolution of a sexual selected trait has two selective influences. First, a correlation between some trait and reproductive success, not due to sexual preference, will develop. Then an additional advantage due to arbitrary female preference will select for those individuals with the distinctive trait. The intensity of the preference and the development of the trait will continue to increase through successive generations as long as the trait is unchecked by strong natural selection pressures, thereby producing a "runaway" effect.

Current theories for sexual selection can be broken down into two broad categories, direct sexual selection and indirect sexual selection (Kirkpatrick & Ryan 1991). Direct selection of mating preference is thought to occur when males with a desired trait provide direct benefits to the female (Kirkpatrick & Ryan 1991). These direct benefits might include food, protection, or high-quality territories. Indirect selection of mating preference is thought to occur when males with desired traits pass on their genetic quality to their offspring (indirectly benefiting females that choose these males). Examples of indirect selection include models such as Fisher's "runaway model", or "good-genes" models such as the Hamilton-Zuk hypothesis of parasite reduction, the "handicap model", or the "truth-in-advertising" hypothesis (Fisher 1930, Zahavi 1975, Hamilton & Zuk 1982, Kodric-Brown & Brown 1984). Good-genes models postulate that females prefer males that have genes that will enhance the viability of their offspring (Kirkpatrick & Ryan 1991). For example, Hamilton and Zuk (1982) suggest that male birds with the most colorful plumage are more resistant to parasites, and are therefore healthier. Females with a preference for the most colorful males will mate with the most disease-resistant males and pass on parasite-resistant genes to their progeny.

The "truth-in-advertising" or honest-indicator hypothesis is another good-genes model. It is based on the observation that there is modest heritable variation in male traits because most variation is correlated with environmental (non-genetic) conditions such as age, nutritional status, social position, and/or parasite load, and that these male traits are costly for individuals to produce and maintain (Kodric-Brown & Brown 1984). Males with bright coloration are demonstrating their genetic quality by displaying traits that indicate that they have acquired essential resources, survived to an advanced age, avoided predation, and have out-competed rivals (Kodric-Brown & Brown 1984). Females with a preference for these males gain mates that will invest in their young and pass on genes that allow their sons to acquire preferable traits. The key to this model is the fact that some male traits are condition-dependent, meaning the physical condition of the individual affects if, or how well, it can produce the trait. In House Finches (*Carpodacus mexicanus*), for example, the ability of a male to find and ingest relatively rare carotenoid pigments during molt, as well as ingest a nutritious diet, directly affects its ability to produce colorful red plumage, which is preferred by females (Hill 1992). Several studies on this particular condition-dependent trait support the hypothesis that ornamentation is an honest-indicator of the quality of the male (Hill 1990, 2002). Therefore, females will preferentially choose the males with the best, or most attractive ornamentation, and thereby increase their fitness.

Birds provide interesting models for studies of sexual selection because their feathers are often brightly colored, and it is believed that diversity in plumage coloration arises from sexual selection (Darwin 1871, for review see Hill & McGraw 2006). The three main types of colors found in the feathers of birds are derived from melanins (black,

gray, and brown), carotenoids (red, orange, and yellow), and structural components of the feather (ultraviolet [UV], blue, and purple) (Shawkey et al. 2003, McGraw et al. 2004, Prum 2006). Although these colors may signal different qualities for different species, it has been shown that carotenoids and structural coloration are condition dependent, and therefore are likely influenced by sexual selection (Hill 2002, Siefferman & Hill 2005a). The condition and colorfulness of the plumage in several species is directly related to the amount of certain nutrients they obtain during molt and is usually associated with the level of parasitic infection (Hamilton & Zuk 1982, Hill 2002). In this way, the amount or quality of the color in the feathers of birds acts as an honest-indicator, or signal, of the quality of the individual.

Structural coloration, which is created by the arrangement of keratin rods in the feather barbs, and can create ultraviolet, blue, or purple feather color, has been shown in many cases to be important for birds in the use of sexual displays and sexual signaling to the opposite sex (Hausmann et al. 2003). Structural coloration is suggested to be a condition-dependent trait that is an honest-indicator of male quality in the Blue Tit (*Parus caeruleus*), the Blue-black Grassquit (*Volatinia jacarina*), the Blue Grosbeak (*Passerina caerulea*), and the Eastern Bluebird (*Sialia sialis*) (Keyser & Hill 1999, Doucet 2002, Johnsen et al. 2003, Shawkey et al. 2003, Siefferman & Hill 2003). In Eastern Bluebirds, studies have shown that males with more intense ultraviolet-blue (UV-blue) plumage provision nestlings more often and fledge more offspring than males with less intense UV-blue plumage (Siefferman & Hill 2003, Siefferman & Hill 2005a). This suggests that the more-ornamented the male, the higher the male's parental investment. Females may be choosing males based on this structurally created UV-blue plumage

because it demonstrates the male's ability to provision offspring and may be an indicator of the likelihood of parental investment.

Parental investment is any investment by the parent in an individual offspring that increases the offspring's chance of survival, at the cost of the parent's ability to invest in other offspring (Trivers 1972). After hatching, the two common forms of parental investment in birds are provisioning nestlings and defending the nest (Clutton-Brock 1991). Although the costs of nestling provisioning accrue slowly, it is more energetically demanding on a parent than nest defense (Trivers 1972, Rytokönen et al. 1995). However, simply measuring energy expended is not a complete approximation of the cost of parental investment. Although provisioning may be more energetically demanding, the other aspect of parental investment, nest defense, has high immediate costs (i.e., it is potentially fatal; Trivers 1972, Brunton 1986, King 1999).

The vast majority of studies of parental investment in birds have quantified different aspects of nestling provisioning rates, such as how they relate to brood size, adult size, nestling size, time of day, season, and parental experience (Nur 1984, Martin 1992, Goodbred & Holmes 1996). Fewer studies have examined aspects of nest defense, such as parental experience, sex of defender, hormone levels, offspring qualities, and nest and predator characteristics (Knight & Temple 1986, Cawthorn et al. 1998, Reyer et al. 1998, Rytokönen 2002; for review see Montgomerie & Weatherhead 1988). Nest defense has been used as the measure of investment to test sexual selection theory in very few cases (Reyer et al. 1998). In fact, only two studies to date have examined both nestling provisioning and nest defense simultaneously in any context (Rytokönen et al. 1995, Duckworth 2006). This is unfortunate because relating the two aspects of parental

investment should give us a better idea of what sort of costs parents are willing to incur for their offspring. One would expect, and theory predicts that provisioning and nest defense are positively correlated, which is what Rytökönen et al. (1995) found in female, but not male, Willow Tits (*Parus montanus*) in Finland.

If provisioning and defense provide a similar assay of investment, then the more-ornamented, male Eastern Bluebirds that better provision their nestlings, as found in previous studies (Siefferman & Hill 2003), should also better defend their nests. This would mean that the structural coloration of male bluebird feathers is an indicator to females of their overall abilities as a parent, and their ability to invest in offspring. However, higher-quality males might not be willing to defend the nest (and incur the risk of injury and death) because high-quality males presumably have more opportunities to find a new mate and re-nest with little cost. Male-ornamentation also may allow them access to more extrapair copulations, which account for 8% to 25% of nestling production (Meek et al. 1994, Gowaty & Plissner 1998).

The purpose of this study is to determine if the two measures of parental investment in Eastern Bluebirds, nestling provisioning and nest defense, are correlated. I will do this by quantifying the frequency of nestling provisioning and measuring the quantity of nest defense behaviors exhibited towards a potential nest predator. I predict that the two forms of parental investment are positively correlated. This study also examines the structural coloration of male Eastern Bluebird feathers to determine if more-ornamented males have higher parental investment. This is performed by measuring the intensity, brightness, chroma, hue and spectral saturation of the UV-blue rump and tail feathers of each male bluebird to obtain a measure of ornamentation, and

correlating these measures with the parental investment, both nestling provisioning and nest defense, of each bird. I predict that the more-ornamented males will invest more in their offspring by provisioning their young at a higher frequency, and exhibiting a higher frequency of defensive behaviors towards a nest predator than the less-ornamented males.

Examining the effort devoted to provisioning nestlings and nest defense can help us understand the costs and benefits that shape patterns of parental investment. Many studies of parental care examine only one form of investment, for example many parental investment studies of birds only examine nestling provisioning. Nest defense, although well studied, is rarely examined in comparison with other measures of parental investment or measures of male quality. Research suggests that in some species more-ornamented males do provision nestlings better, and therefore invest more in their offspring. However, the other, more risky aspect of parental investment, nest defense, has not been examined in regards to male ornamentation. Ultimately this research will help us better understand sexual selection and the evolution of parental care.

METHODS

Study Species. The Eastern Bluebird (*Sialia sialis*) is a small, vibrantly colored, sexually dimorphic thrush that occurs in most of the central and eastern United States (Gowaty & Plissner 1998). Males typically have bright blue plumage on the head, back, wings, rump, and tail; the chest of the male is chestnut-brown, and the belly is white. Females are typically drabber, with a gray-blue coloration on the head, back, wings, rump, and tail; the chest is also chestnut-brown, and the belly white (Gowaty & Plissner 1998, Siefferman & Hill 2003). The Eastern Bluebird is an obligate secondary-cavity nester that breeds from late March through early August in the southeastern U.S. (Gowaty & Wagner 1988). Bluebirds are socially monogamous with biparental care of the nestlings. Females typically lay four to five eggs in each clutch and can have up to three clutches per breeding season (Gowaty & Plissner 1998). Females incubate the eggs for 14 days on average; after hatching the male and female feed the nestlings until they fledge between 16 and 19 days of age (Gowaty & Plissner 1998).

My study was conducted from April through August, during the summer of 2006 (with pilot work during the summer of 2005). The study sites were in Bulloch County, Georgia, near the city of Statesboro (ca. 32° 26' N; 81° 46' W). I placed 40 wooden nestboxes in suitable habitat at three sites: one in northern Bulloch County and two just south of Statesboro (Figure 1; for site descriptions see Appendix A). Bluebird boxes were placed on metal poles, approximately 1.5-m high, with PVC baffles (5.1-cm diameter) to deter predators. The nestboxes had a floor of approximately 10.2 cm x 10.2 cm, a 3.8-cm diameter opening, and a removable lid. I checked nestboxes for nesting activity (approximately every 3 days) throughout the season. Boxes with completed nests

were checked daily for egg-laying activity. I recorded the date on which the first egg was laid, the date of hatching, the number of offspring, and the date nestlings fledged for each nest. Each nestling was weighed and had their tarsus length measured to the nearest 0.1 cm when they were approximately 14 days old.

Male and female bluebirds were captured with a mist net near the end of the incubation period or just after the nestlings hatched. I banded all captured birds with a unique set of color bands, so they could be identified by sight. Standard body measurements were taken from each adult, including mass, unflattened wing chord, and tarsus length to the nearest 0.1 cm. The age of the bird was estimated as either second year or after-second year by the condition of the tenth primary (Pitts 1985). Eastern Bluebirds do not molt their rectrices, remiges, and primary coverts during their first prebasic molt, so age can be estimated by examining the wear, fraying, and coloration of the 10th primary covert through their first year. I collected nine rump feathers and the two outer rectrices and placed them into separate envelopes for each bird.

I quantified provisioning rates (rates at which parents delivered food to the nest) for each pair of bluebirds during the nestling stage when chicks were 7 - 9 days of age. I sat in a blind at 30 - 50 m distance and observed the nest with a 20x spotting scope for approximately 1 hour each during the morning hours. Parental provisioning of nestlings was quantified as the number of feeding trips by each sex per chick per hour.

Nest defense experiments were conducted when the nestlings were 7 - 9 days old. I elicited defense behaviors from bluebird parents by placing a Black Racer (*Coluber constrictor*) or an Eastern Rat Snake (*Elaphe alleghaniensis*; both approximately 1.5 m in length) on the ground within 1 m of the nestbox for 10 minutes. Eastern Rat Snakes and

Black Racers are common in the southeastern U.S., both are predators of bird eggs and nestlings, and are predators of the Eastern Bluebird (Hamilton & Pollack 1956, Conant & Collins 1998, Gowaty & Plissner 1998). Snake predators can account for up to 40% of nest depredation (Gowaty & Plissner 1998), and in pilot work, virtually all of the nests on un-baffled poles were depredated, most likely by snakes. I placed the snake inside a clear plexiglass container, approximately 36.5-cm wide, 54.6-cm long, and 13.2-cm high, allowing the snake to move freely and be seen from all angles. The container with the snake was hidden under a camouflaged cloth attached to a monofilament string held by the observer inside a blind 30 - 50 m away from the nest. At a time selected randomly, anywhere from 5 - 15 minutes after I returned to the blind, the cloth was pulled away and the snake revealed (Cawthorn et al. 1998). The latency period was calculated and recorded as the amount of time between revealing the snake and the first approach by a bluebird to the nest site. Agonistic behaviors, including the number of puff-ups, beak rubs, standing alerts, chatters, wing-flickers, flybys, hovers, lands on the nestbox, approaches within 1 m, dives at the snake, lands on the ground, and strikes at the snake were counted for each sex (see detailed description in Table 1; Krieg 1971, Knight & Temple 1986, Gowaty & Plissner 1998). After 10 minutes, the snake was removed. Birds that did not come to the nest site during the 10 minute bout were not included in the analysis.

I analyzed feather color by taping all of the feathers to a piece of black construction paper and measuring reflectance of the feathers. The nine rump feathers were individually taped so they overlapped in the same manner as they would on a bird, and the two rectrices were taped individually. I measured spectral data with an Ocean

Optics S2000 spectrometer, with a deuterium-tungsten-halogen lamp and fiber optic probe, between 300 nm and 700 nm (see detailed methods in Siefferman & Hill 2003). I sampled each set of rump feathers five times and the two outer rectrices six times, moving the probe a minimum 4 mm for each sample. The five rump samples were averaged together and the six rectrix samples were averaged together to obtain the rump and tail spectral measurements for each bird.

I quantified five color variables - intensity, brightness, chroma, hue, and spectral saturation - for the UV-blue colored rump and tail for each bird (Figure 2). Intensity is the amount of reflectance of the feathers at the maximal (or hue) wavelength. Brightness is a measure of the total reflectance of the feathers between the ranges of 300 nm and 700 nm. Chroma is the proportion of the reflectance in the range of interest (UV-blue ranges from approximately 300 nm to 500 nm) to the total reflectance between 300 nm and 700 nm (Siefferman & Hill 2003). Hue is the wavelength at which the greatest amount of light is reflected. Spectral saturation is a measure of the proportion of light reflected within a range of 50 nm on either side of the maximum hue to the total reflectance between 300 nm and 700 nm (Shawkey et al. 2003). I averaged each of the five spectral variables from the rump and tail of each bird to obtain the overall UV-blue coloration for each bird.

Statistical analysis. I compared log-transformed, paired provisioning rates (provisions/chick/hour) for males and females with a paired t-test and a Pearson's correlation coefficient. Frequency of nest defense behaviors was divided by the duration of each defense bout, after latency was removed, to obtain the rate of each defense behavior per minute. Paired male and female nest defense rates (behaviors/minute) were

compared with a Wilcoxon sign-rank test, and a Spearman's rank correlation to test for differences in male and female behavior and to examine their relationships.

Nestling provisioning is depreciable, meaning the benefit to each nestling declines with increasing brood size. Nest defense can be considered non-depreciable (Rytokönen et al. 1995) because the benefits of defense by the parents are equal for each nestling. Thus, I quantified the relationship between defense and provisioning by correlating mean provisioning per chick per hour with overall rate of nest defense behaviors. However, parental effort devoted to provisioning and defense might both be influenced by brood size (regardless of whether benefits to nestlings are depreciable or not). Thus, I also correlated mean provisioning rates per hour with overall rate of nest defense.

To assure independence, for all bluebirds that fledged multiple broods, mean provisioning rates and mean defense rates (behaviors/minute) were used in the analysis. I quantified the relationship between nest defense behaviors (behaviors/minute) and the mean provisioning rates (provisions/chick/hour and provisions/hour) using a Spearman's rank correlation coefficient for both sexes. A principal component analysis (PCA) was performed on the mean rates of nest defense for male bluebirds, excluding the behaviors alert, flyby, approach (1m), dive, land, and strike, as only one or no males performed these behaviors. A PCA was performed on the mean rates of nest defense for female bluebirds, excluding the behaviors puff-up, beak rub, alert, approach (1m), dive, land, and strike, as only one or no females performed these behaviors. Separate principal component analyses were performed for each sex because there was not enough overlap in the behaviors performed by each sex, so a combined PCA could not capture the variation in defense. I compared the male and female principal components of nest

defense with their log-transformed mean provisioning rates (provisions/chick/hour and provisions/hour) using a Pearson's correlation coefficient.

The spectral measurements from the five color variables were compared with a Pearson's correlation coefficient to look for relationships between the variables (Sokal and Rolf 1995). A principal component analysis was performed on the color measurements to extract the dominant dimensions of variation from the color measurements and define new, composite variables from the original five color variables. Principal component analysis is a statistical technique that is used to condense a large number of original variables into a smaller set of new composite variables, with little loss of information (McGarial et al. 2000). PCA provides an interpretation of the new variables based on the five original variables by providing a measure of how much weight each original variable has on the new variables. In essence, a PCA of these five color variables provided new variables that can be used to easily assess the degree of ornamentation of each male bluebird.

I compared mean nestling age to the mean provisioning rates with a least squares regression for males to obtain the residuals. Age-adjusted mean provisioning rates for each male were compared with male ornamentation (principal components) using a Pearson's correlation coefficient. I compared the individual behaviors of nest defense with male ornamentation using a Spearman's rank correlation. I compared the principal components of nest defense with male ornamentation, using a Pearson's correlation coefficient. All means are expressed \pm 1 standard error.

RESULTS

I observed a total of 43 nests initiated by 21 different pairs of Eastern Bluebirds. Sixteen nests failed to hatch eggs, but 24 of the 27 (88.9%) nests that hatched nestlings successfully fledged offspring. Of the 21 bluebird pairs, 13 male and 18 female bluebirds were captured, banded, and had feather samples collected for analysis. A mean of 4.42 ± 0.12 eggs was laid in each nest for a total of 168 eggs; a mean of 3.25 ± 0.27 nestlings was fledged from each successful nest for a total of 78 nestlings fledged. Nest defense and nestling provisioning observations were performed on 19 of the 21 bluebird pairs (including 11 banded males and 14 banded females) and 25 of the 27 nests that hatched nestlings.

Parental investment

On average, male Eastern Bluebirds provisioned nestlings 1.88 ± 0.24 times per chick per hour ($n = 24$), while female bluebirds provisioned nestlings 1.93 ± 0.20 times per chick per hour ($n = 25$). For bluebird pairs, there was no significant difference in provisioning between pair members (paired $t = 0.24$, $n = 24$, $p = 0.81$; log-transformed), and there was no correlation between male and female provisioning rates ($r = 0.27$, $n = 24$, $p = 0.20$; log-transformed; Figure 3).

The sexes differed slightly in parental investment as measured by nest defense. Males performed many agonistic behaviors when confronted with the potential nest predator (Table 2). The defensive behaviors performed the most often by male bluebirds were the wing-flicker and chatter, few males performed the alert, flyby, approach, dive, and land behaviors, and no males struck at the predator. Females performed fewer agonistic behaviors but only wing-flicker differed significantly (Table 2). The most

common behavior performed by female bluebirds was the chatter, and no females approached, dove, landed near, or struck at the predator. Most of the rates of nest defense behavior were not correlated between males and females, although the rate of beak rub was positively correlated and the rate of hover had positive trends (Table 2).

Nestling provisioning and nest defense

Separate principal component analyses were performed for male and female Eastern Bluebirds on the rates of nest defense behaviors to extract the dominant gradients of variation. For males, the first principal component (PC1) was positively related to the behaviors puff-up, beak rub, chatter, and hover, and explained 48% of the variation in the original data set (Table 3). Males with large PC1 scores performed puff-up, beak rub, chatter, and hover behaviors at higher rates. For females, PC1 was positively related to the behaviors wing-flicker, flyby, and hover, and explained 42% of the variation in the original data set (Table 4). Females with large PC1 scores performed wing-flicker, flyby, and hover behaviors at higher rates.

The individual rates of nest defense (behaviors/minute) were not correlated with either measure of nestling provisioning (provisions/chick/hour or provisions/hour) for either sex (Table 5; Table 6). In addition, no significant correlations were detected when the principal component of nest defense was compared with the mean provisions/chick/hour ($r = 0.13$, $n = 11$, $p = 0.70$; log-transformed) or mean provisions/hour ($r = 0.50$, $n = 11$, $p = 0.12$; log-transformed) for male bluebirds. Female bluebirds also showed no correlation between the principal component of nest defense and mean provisions/chick/hour ($r = -0.01$, $n = 13$, $p = 0.98$; log-transformed) or provisions/hour ($r = 0.04$, $n = 13$, $p = 0.91$; log-transformed).

Plumage color

The five color variables obtained from the spectral analysis of rump and tail feathers of the male bluebirds (intensity, brightness, UV-blue chroma, hue, and saturation) were highly correlated (Table 7). A PCA was performed on the color measurements to extract the dominant gradients from the color measurements. The first two principal components were selected to be used in further analysis because they explained the majority of the variation of the color variables. The first principal component (PC1) was strongly related to all five of the original color variables and explained 86% of the variation in the original data set. The second principal component (PC2) was strongly related to brightness and hue and explained 11% of the variation (Table 8). Principal component 1 is an axis describing overall plumage ornamentation; males with larger PC1 scores had UV-blue plumage with more intensity, brightness, chroma, saturation, and had a hue that was shifted more into the UV range. Principal component 2 is an axis describing plumage brightness and hue; males with large PC2 scores had UV-blue plumage that was brighter and had a hue that was shifted more into the blue range.

Nestling provisioning and ornamentation

Mean provisioning rates for males were compared with the age of the nestlings at the time provisioning observations were performed. Although there was no significant effect of nestling age on mean provisioning rates ($R^2 = 0.13$, $F_{1,9} = 1.38$, $p = 0.27$; Figure 4), there was a trend that older nestlings were provisioned at a higher rate. To remove the effect of nestling age on provisioning rates, the provisioning rates for males were measured as the residuals from the regression of mean provisioning rate on nestling age.

Neither overall male ornamentation (PC1) nor brightness/hue (PC2) was correlated with the age-adjusted mean provisioning rate of male bluebirds. However, male brightness/hue (PC2) did have a strong positive trend when correlated with the age-adjusted mean provisioning rate ($r = 0.57$, $n = 11$, $p = 0.07$; Figure 5). Males with brighter and bluer (hue shifted further into the blue region) plumage tended to provision their nestlings at a higher rate.

Nest defense and ornamentation

Male ornamentation was negatively correlated to a few of the rates of nest defense (behaviors/minute). More-ornamented males (high PC1) tended to perform the puff-up and beak rub behaviors at slower rates, and brighter males (high PC2) performed chattering and hovering behaviors at significantly slower rates (Table 9). Male ornamentation tended to be negatively correlated with the principal component of nest defense rates. More-ornamented males (high PC1) tended to perform nest defense behaviors (puff-up, beak rub, chatter, and hover) at a lower rate ($r = -0.71$, $n = 7$, $p = 0.07$; Figure 6). Male brightness/hue (PC2) was not related to the nest defense measures ($r = -0.21$, $n = 7$, $p = 0.65$).

Although neither nestling provisioning nor nest defense was significantly correlated with male ornamentation, there were strong trends in both cases. If we assume that the principal components of male ornamentation (PC1 and PC2) are both measures of ornamentation of male bluebirds, then we can compare the correlation of provisioning and ornamentation to the correlation of defense and ornamentation. This allows us to ascertain that while individually, the correlations are not significantly different than zero, the two correlations are significantly different from each other ($p < 0.01$).

DISCUSSION

Although parental investment is a key variable in evolutionary theory and sexual selection theory, few studies address more than one component of investment. In birds, investment is almost always measured as the amount or rate of provisions provided to nestlings. Nest defense, another important component of parental investment in birds, is seldom examined in comparison to nestling provisioning. Some authors have addressed how provisioning and defense should be related in theory (Trivers 1972, Clutton-Brock 1991, Martin 1992), but few studies to date have measured these two components of investment in tandem, and it is unknown if these two measures of investment yield similar patterns in real populations.

My results permit three main conclusions. First, nestling provisioning and nest defense were not correlated. I expected that provisioning and nest defense would be positively correlated; individuals that fed their nestlings at a higher rate (high investment) should also perform nest defense behaviors at a higher rate (high investment). A positive correlation would be expected based on two perspectives. First, parental investment theory predicts that well-provisioned nestlings, of high value to the parent, should receive a greater amount of protection from a potential predator in the form of increased nest defense (Trivers 1972, Rytökönen 2002). In other words, parents should be willing to protect their investment. Second, it has been suggested that high-quality males (more-ornamented males) are signaling their willingness or ability to invest in offspring. Presumably this willingness to invest should be detectable regardless of the measure of parental investment (Siefferman & Hill 2003). This was not the case in my study.

Eastern Bluebirds may be varying their levels of parental investment based on the costs, benefits, and risks associated each type of investment. Nestling provisioning is more energetically costly in the sense that parents must provision their nestlings regularly over a long period of time (Clutton-Brock 1991). Provisioning therefore accrues benefits and costs at a slow rate and is not considered risky. On the other hand, nest defense can be extremely risky, and the costs and benefits of the individual's actions are immediate. Bluebirds may be assessing the large difference in risk associated with nest defense versus provisioning and this, in turn, might result in distinctly different patterns of effort devoted to the two behaviors.

Whatever the reason for the lack of correlation between nest defense and nestling provisioning in bluebirds, it is becoming clear that this pattern may be widespread. For example, Rytokönen et al. found that there is no association between nest defense intensity and provisioning for male Willow Tits (1995). A study of the effects of testosterone on nest defense behaviors of the Dark-eyed Junco (*Junco hyemalis*) has shown that males with extra testosterone do not decrease the intensity of nest defense, despite the fact that these males do reduce provisioning of nestlings (Cawthorn et al. 1998). Finally, Duckworth found that male Western Bluebirds (*Sialia mexicana*) show no associations between nest defense and provisioning (2006). This means that we may see different patterns of parental investment depending on the variable we use to measure investment. Future studies must consider that their choice of parental investment measure has consequences. Although some authors (Martin 1992, Rytokönen et al. 1995) suggest that there may be other important measures of parental investment after hatching, such as nest guarding (which may also be comparable to nestling provisioning in terms of

costs and risk), it is safe to say, based on this growing body of literature, that nestling provisioning and nest defense are not equivalent measures of parental investment.

A second important result of my study is the observation that male ornamentation did predict rates of nestling provisioning. This is consistent with sexual selection theory, which predicts that measures of parental investment should be related to condition-dependent ornamentation (Hill & McGraw 2006). I found that the brightness of the UV-blue rump and tail feathers of the male Eastern Bluebird tends to be positively correlated with nestling provisioning, which is consistent with other studies of Eastern Bluebirds (Siefferman & Hill 2003). This trend for males with better plumage coloration to provision nestlings at a higher rate is also found in Blue Grosbeaks, another bird with UV-blue structural coloration (Keyser & Hill 2000). Females may be using this plumage trait as an indicator of male quality, and his willingness or ability to provision young. This is consistent with the truth-in-advertising model of sexual selection.

Finally, I found that a second measure of parental investment, nest defense, was not greater in more-ornamented males. If anything, my study is the first to demonstrate that there was a tendency toward less investment in nest defense by more-ornamented males. I predicted that more-ornamented males would perform nest defense behaviors at a higher rate, as predicted by the truth-in-advertising hypothesis and observed in House Sparrows (*Passer domesticus*) where males with larger chest patches tend to approach and attack a potential nest predator more than males with smaller chest patches (Reyer et al. 1998). Instead, I found that more-ornamented males performed agonistic behaviors at slower rates. It appears that overall, male bluebirds in this population were less willing to perform the high-risk behaviors of nest defense when presented with a snake predator.

My results suggest that more-ornamented males may not be willing to invest in nest defense because they may have greater future reproductive options. More-ornamented males have been shown to nest earlier, obtain limited nestboxes, attempt more broods, fledge more offspring, and likely have more extra-pair copulations than less-ornamented males (Siefferman & Hill 2003, Siefferman & Hill 2005a, Siefferman & Hill 2005b). These future reproductive options, which are presumably not available to less-ornamented males, may influence the more-ornamented males to be less risk prone and therefore invest less in nest defense. Conversely, less-ornamented males may need to be more risk prone in an effort to protect limited reproductive options, and potentially are more aggressive in general in an effort to protect their territories and mates from higher-quality males.

It is important to remember that bluebirds may vary their behaviors in response to different types of intruders and predators (Gowaty & Wagner 1988, Gowaty & Plissner 1998). More-ornamented males may not be willing to risk their lives, particularly against a snake predator for which there may be a low probability of success. This study examined nest defense towards a snake predator, not an avian nest competitor, and bluebirds may be able to regulate the level and type of aggressive responses accordingly when exposed to different stimuli. It may be that defense against a snake has a low probability of success, and therefore more-ornamented males are less aggressive (less risk prone) towards the predator. However, in other contexts, such as defending the nest from a nestbox competitor (House Sparrow or Tree Swallow for example), more-ornamented bluebirds may exhibit different levels of agonistic behaviors to protect their nesting site.

In summary, the patterns of parental investment we observe in a particular species may depend on our measure of investment. Specifically, in regards to condition-dependent plumage, I observed opposite patterns of parental investment when examining two different measures of investment. This suggests that condition-dependent traits do not always predict the same patterns when examined with different forms of parental investment. Future studies of parental investment must realize the costs and risks associated with the different measures of investment will influence parental behavior and may yield different results based on the measure of investment.

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Table 1. An ethogram of agonistic behaviors of male and female Eastern Bluebirds measured during nest-defense experiments (adapted from Krieg 1971, Gowaty & Plissner 1998).

Behavior	Description
Puff-up	The feathers are fully erect and the body has a ragged appearance with broken outline
Beak Rub	Head down to the perch, rapid rubbing of beak on alternating sides of perch
Alert	Stands erect with body feathers sleeked, extension of the neck upwards
Chatter	Vocalization: loud continual "chit-chit-chit" uttered in rapid succession
Wing-Flicker	Perches in oblique position and rapidly flicks both wings out completely and back to body
Flyby	Flies from perch towards the nestbox, not landing, quickly flies back up to perch; usually accompanied by chatter
Hover	Flies to nestbox, not landing; hovers above predator
On Box	Flies and lands on nestbox, usually inspects predator
Approach (1m)	Flies to within 1 m of predator
Dive	Hovers in midair, chattering, then dives quickly while snapping bill, flies up and hovers in midair to begin dive again
Land	Lands on ground within 1 m of predator
Strike	Dives far enough down to strike predator with feet and claws

Table 2. Mean (± 1 standard error) rates of behaviors per minute for each of the twelve nest defense behaviors quantified for male ($n = 14$) and female ($n = 17$) Eastern Bluebirds. Male and female rates were paired by nest, compared with a Wilcoxon sign-rank test, and correlated with a Spearman's rank correlation.

Behavior	Mean \pm SE		Wilcoxon sign-rank		Correlation	
	Males	Females	z	p	r_s	p
Puff-up	0.05 \pm 0.02	0.03 \pm 0.03	5.0	0.13		
Beak Rub	0.09 \pm 0.04	0.05 \pm 0.05	2.0	0.63	0.57	0.05
Alert	0.02 \pm 0.02	0.02 \pm 0.02	2.0	0.50	-0.13	0.68
Chatter	0.25 \pm 0.16	0.43 \pm 0.31	2.5	0.69	0.02	0.96
Wing-Flicker	0.30 \pm 0.10	0.08 \pm 0.04	14.0	0.02	0.48	0.12
Flyby	0.04 \pm 0.04	0.10 \pm 0.06	2.0	0.50	-0.13	0.68
Hover	0.16 \pm 0.09	0.03 \pm 0.02	6.5	0.13	0.53	0.08
On Box	0.03 \pm 0.02	0.13 \pm 0.08	3.5	0.44	0.32	0.31
Approach (1m)	0.03 \pm 0.03	0.00				
Dive	0.10 \pm 0.10	0.00				
Land	0.02 \pm 0.02	0.00				
Strike	0.00	0.00				

Table 3. Principal component analysis, including factor loadings, of the mean rates of nest defense behaviors performed by male Eastern Bluebirds (n = 11).

Variable	Principal Component	
	1	2
Puff-up	0.528	0.355
Beak Rub	0.381	0.582
Chatter	0.514	-0.278
Wing-flicker	0.121	-0.510
Hover	0.517	-0.279
On Box	-0.172	0.348
Eigenvalue	2.89	1.30
Percent Variation	48.2	21.7
Cumulative Variation	48.2	69.9

Table 4. Principal component analysis, including factor loadings, of the mean rates of nest defense behaviors performed by female Eastern Bluebirds (n = 13).

Variable	Principal Component	
	1	2
Chatter	-0.097	0.691
Wing-flicker	0.377	0.343
Flyby	0.616	-0.184
Hover	0.632	-0.165
On Box	-0.264	-0.587
Eigenvalue	2.09	1.21
Percent Variation	41.8	24.4
Cumulative Variation	41.8	66.1

Table 5. Spearman's rank correlation coefficients for male Eastern Bluebird provisioning rates (provisions/chick/hour and provisions/hour) and the rates of nest defense (behaviors/minute; n = 11).

	Provisions/chick/hour		Provisions/hour	
	r_s	p	r_s	p
Puff-up	0.16	0.63	0.40	0.22
Beak Rub	0.14	0.68	0.36	0.28
Chatter	-0.26	0.43	0.09	0.80
Wing-Flicker	0.19	0.58	0.23	0.49
Hover	-0.20	0.56	0.23	0.49
On Box	-0.17	0.63	-0.12	0.73

Table 6. Spearman's rank correlation coefficients for female Eastern Bluebird provisioning rates (provisions/chick/hour) and rates of nest defense (behaviors/minute; n = 13).

	Provisions/chick/hour		Provisions/hour	
	r_s	p	r_s	p
Chatter	-0.04	0.89	-0.10	0.74
Wing-flicker	-0.41	0.17	-0.41	0.17
Fly-by	0.10	0.74	-0.07	0.83
Hover	0.08	0.80	-0.07	0.83
On Box	0.29	0.35	0.23	0.45

Table 7. Pearson's correlation coefficients of the combined UV-blue rump and tail color variables for male Eastern Bluebirds (n = 13).

* p < 0.05, ** p < 0.01, *** p < 0.001

	Intensity	Brightness	Chroma	Hue
Brightness	0.99***			
Chroma	0.90***	0.89***		
Hue	-0.66*	-0.59*	-0.81***	
Saturation	0.83***	0.76**	0.87***	-0.90***

Table 8. Principal component analysis, including factor loadings, of the five color variables for male Eastern Bluebirds (n = 13).

Variable	Principal Component	
	1	2
Intensity	0.459	0.391
Brightness	0.442	0.529
Chroma	0.467	0.032
Hue	-0.411	0.677
Saturation	0.454	-0.330
Eigenvalue	4.29	0.56
Percent Variation	85.8	11.2
Cumulative Variation	85.8	97.0

Table 9. Spearman's rank correlation coefficients for male Eastern Bluebird overall ornamentation (PC1) and brightness/hue (PC2) and the rates of nest defense (behaviors/minute; n = 7).

	Ornamentation (PC1)		Brightness (PC2)	
	r_s	p	r_s	p
Puff-up	-0.70	0.08	0.04	0.94
Beak Rub	-0.74	0.06	0.18	0.69
Chatter	0.02	0.97	-0.87	0.01
Wing-Flicker	0.21	0.64	-0.03	0.94
Hover	-0.11	0.81	-0.78	0.04
On Box	0.22	0.63	0.18	0.70

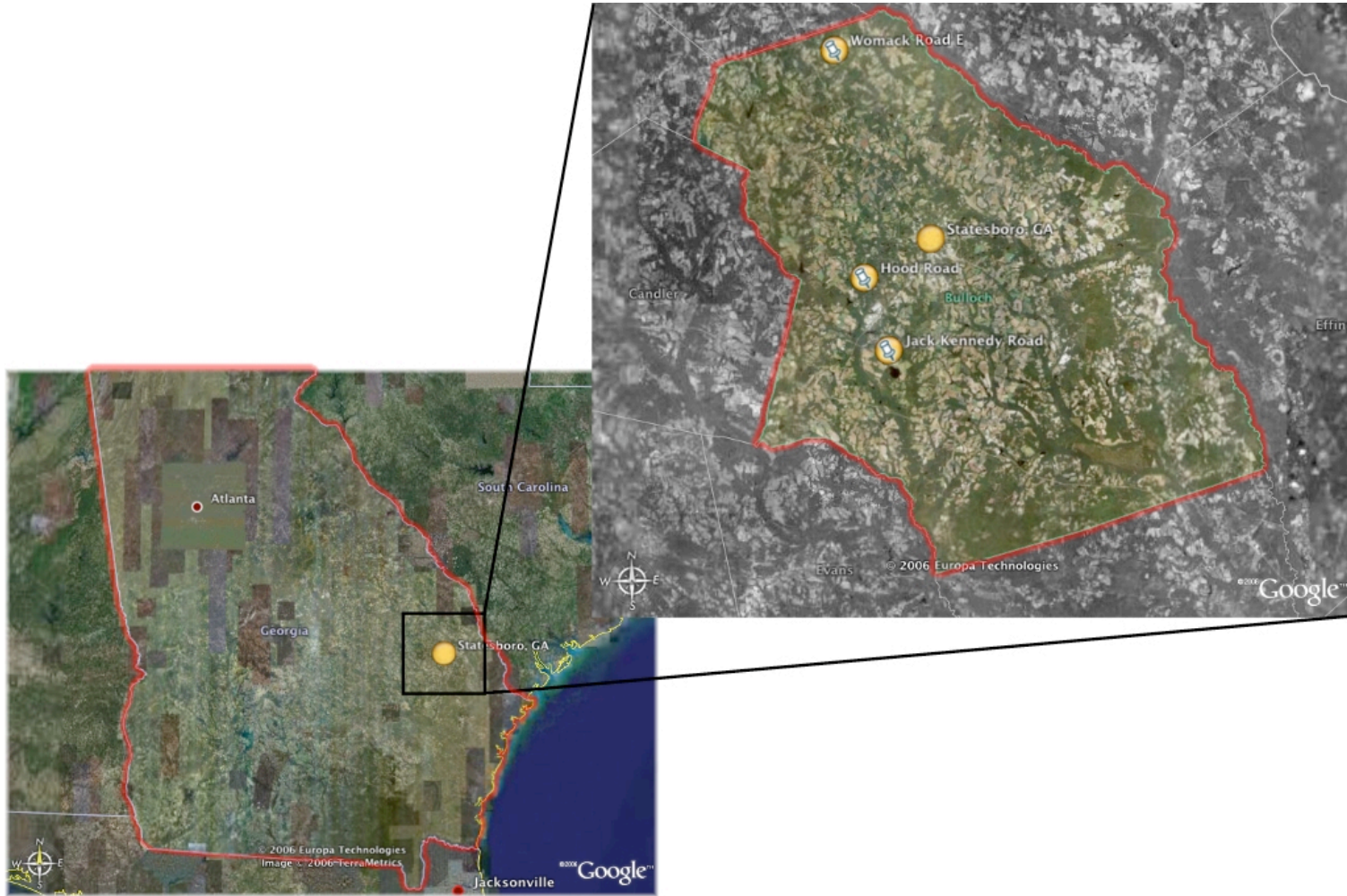


Figure 1. Map of Georgia and Bulloch County, showing the three study sites at Womack Road East, Jack Kennedy Road, and Hood Road. Maps courtesy of Google Earth™.

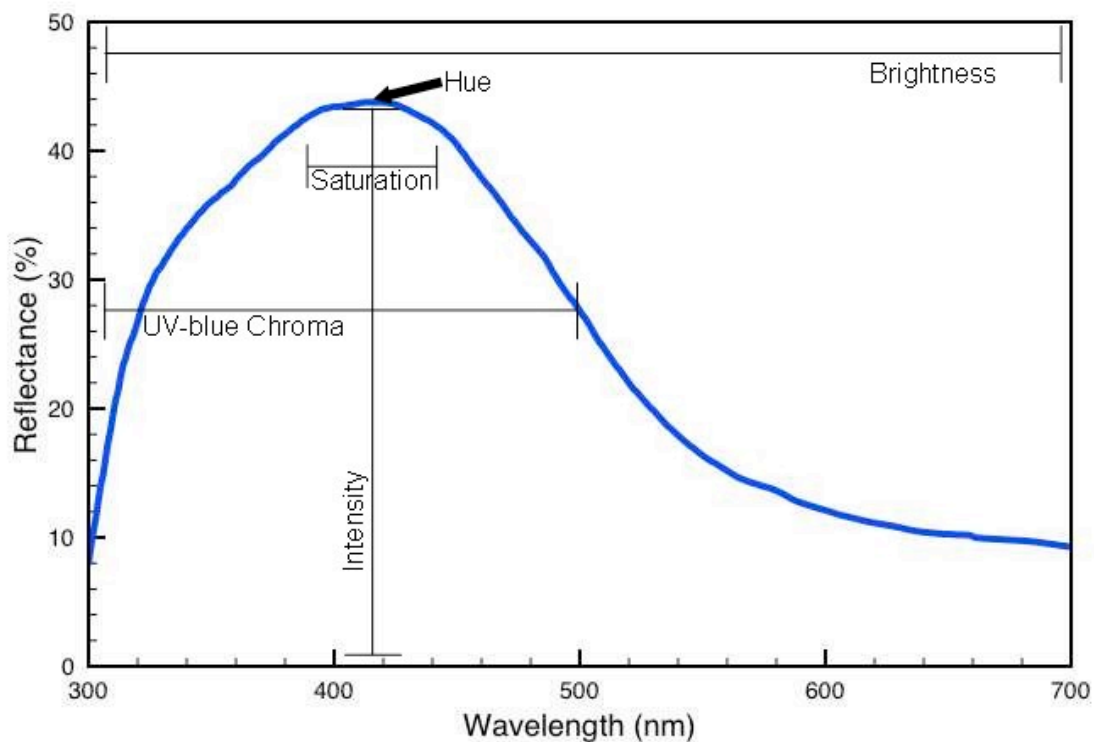


Figure 2. Reflectance spectra from the rump feathers of a male Eastern Bluebird. Intensity is a measure of the reflectance at the maximum wavelength, brightness is the total reflectance between 300 – 700 nm, UV-blue chroma is the reflectance in the UV-blue range divided by the total reflectance, hue is the maximum wavelength, and saturation is the reflectance within 50 nm of the maximum wavelength divided by total reflectance.

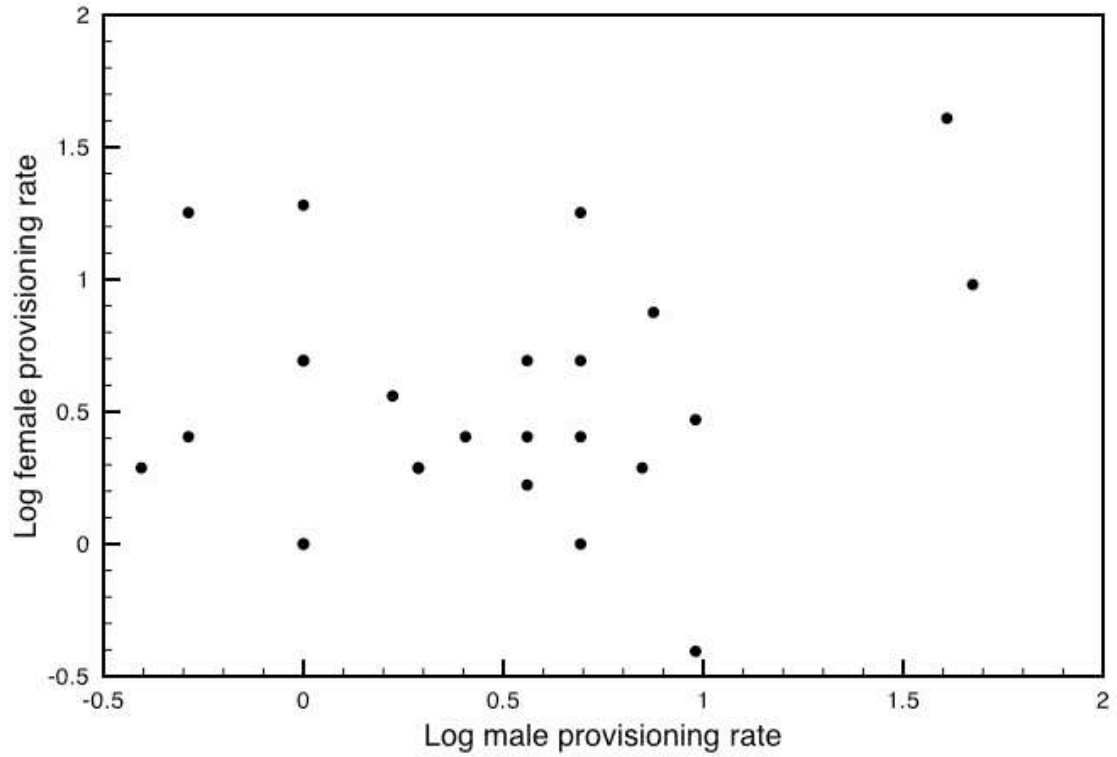


Figure 3. Male Eastern Bluebird provisioning rates (provisions/chick/hour) were not correlated with female bluebird provisioning rates ($r = 0.27$, $n = 24$, $p = 0.20$; log-transformed).

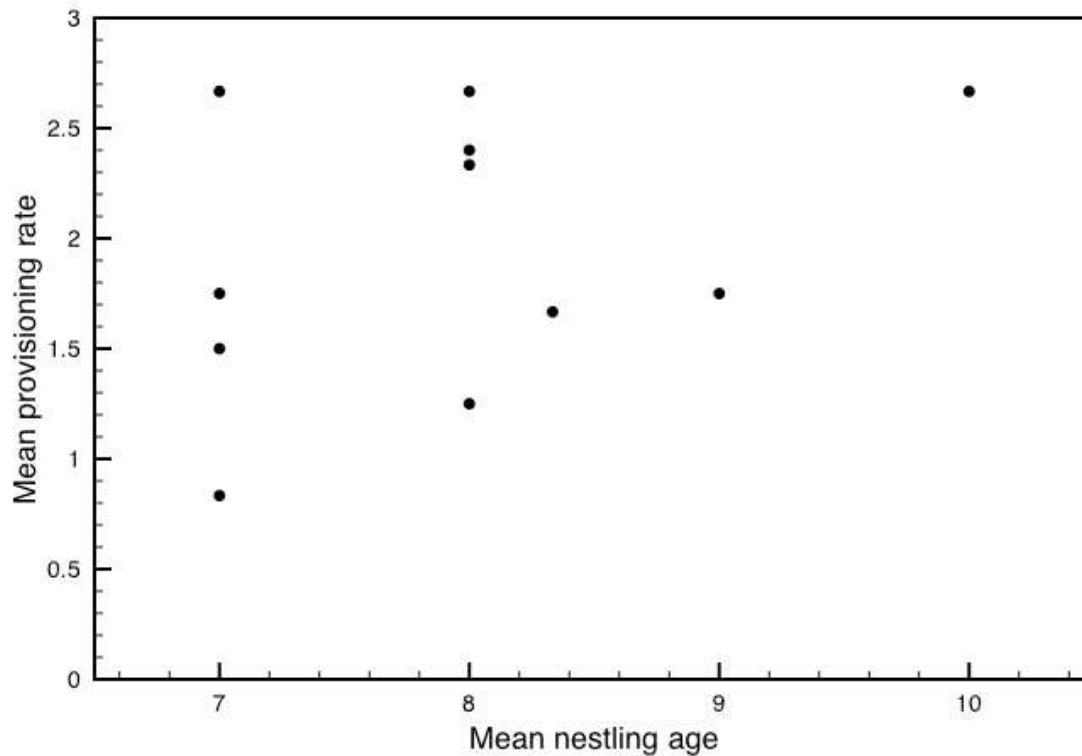


Figure 4. The relationship between mean nestling age and mean provisioning rate per chick per hour by male Eastern Bluebirds. Provisioning rates did not vary significantly with nestling age ($R^2 = 0.13$, $F_{1,9} = 1.38$, $p = 0.27$).

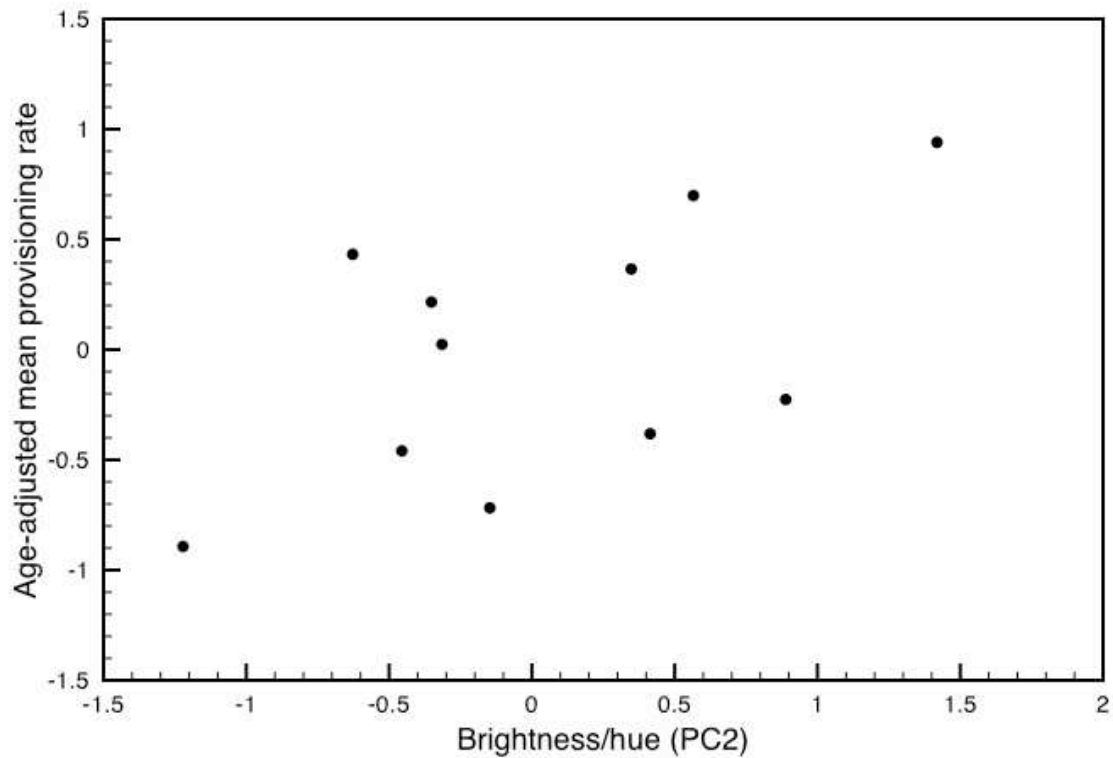


Figure 5. Age-adjusted mean provisioning rate (provisions/chick/hour) tended to be positively correlated with brightness/hue (PC2) for male Eastern Bluebirds ($r = 0.57$, $n = 11$, $p = 0.07$).

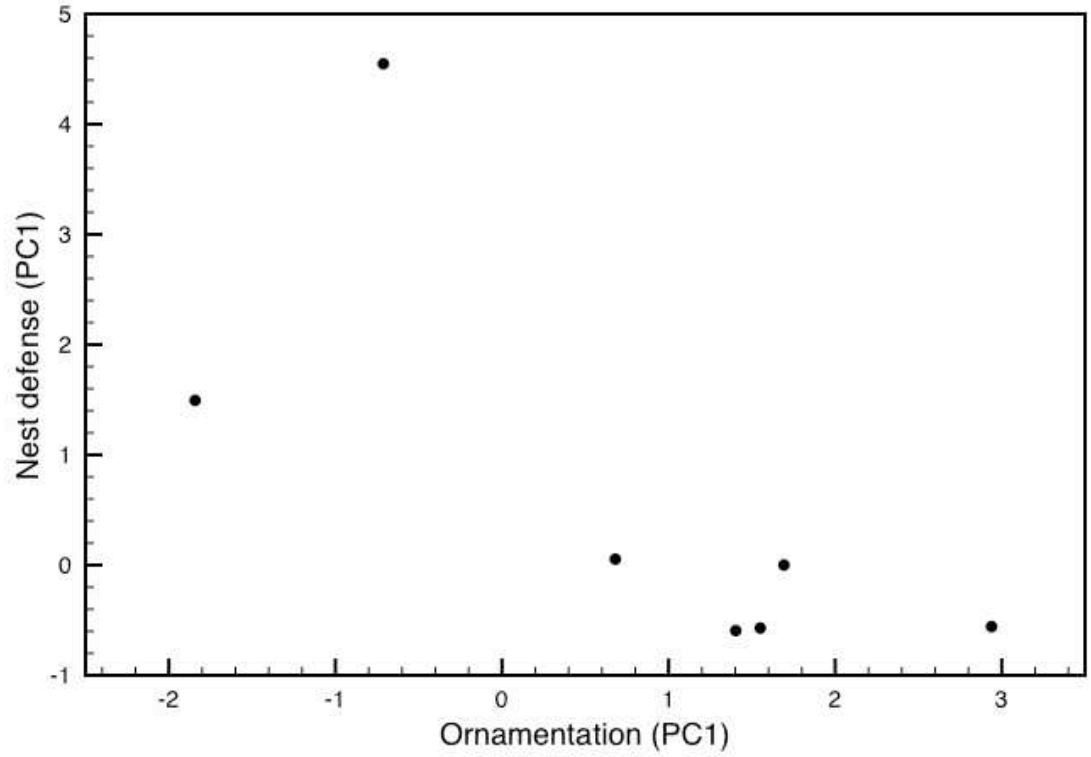


Figure 6. Overall ornamentation (PC1) tended to be negatively correlated with the rates of nest defense (PC1) for male Eastern Bluebirds ($r = -0.71$, $n = 7$, $p = 0.07$).

APPENDIX A
STUDY SITE DESCRIPTIONS

Site 1:

GPS Coordinates: 32° 37.105' N
 81° 52.838' W

This study site was located off of Womack Road East, in northern Bulloch County, GA. The site is approximately 110 acres of privately owned woodland and open fields. Twenty bluebird boxes are situated around the open fields on this land and neighboring fields.

Site 2:

GPS Coordinates: 32° 25.103' N
 81° 51.172' W

This study site was located off of Jack Kennedy Road, just south of Statesboro, in Bulloch County, Georgia. The site is approximately 62 acres of privately owned land consisting mainly of open fields, small agricultural plots, and woodlands. Eight bluebird boxes are situated around the open fields and small agricultural plots on this land.

Site 3:

GPS Coordinates: 32° 21.103' N
 81° 49.637' W

This study site was located off of Hood Road, just southwest of Statesboro, in Bulloch County, Georgia. The site is approximately 22 acres of privately owned land consisting of open grassland and young pine trees. Ten bluebird boxes are located on this property.