SEXUAL SELECTION ON PLUMAGE COLOR IN A NORTH CAROLINA POPULATION OF EASTERN BLUEBIRDS

by

Callie Lynn Younginer

Honors Thesis

Appalachian State University

Submitted to the Department of Biology
in partial fulfillment of the requirements for the degree of

Bachelor of Science

May 2018

Approved by:

Lynn Siefferman, Ph. D., Thesis Director

Michael Osbourn, Ph. D., Second Reader

Lynn Siefferman, Ph. D., Biology Department Honors Director

Sexual Selection on Plumage Color in a North Carolina Population of Eastern Bluebirds

Callie Younginer

Dr. Lynn Siefferman

Abstract

Throughout nature, species exhibit exaggerated ornamentation that aids in the securement of mates. Sexual selection acts on variation in mating success and is prevalent in the color of plumage of many species of birds. Sexual dimorphism exists in species with conventional sex roles, but in species with comparable amounts of parental investment, females and males are often similarly colored. Male mate choice and/or female competition may explain this ornamentation in females. Eastern bluebirds (*Sialia sialis*) are a socially monogamous passerine with biparental care that display sexually dichromatic coloration; males have brilliant blue head and rump plumage and chestnut breasts while females have duller color. In both male and female eastern bluebirds, studies have provided evidence that the UV-reflectance in their blue plumage is a product of sexual selection as more ornamented individuals experience higher reproductive success (Siefferman & Hill 2003, 2005a; Hubbard 2009). In this study, I used a 9-year dataset to explore evidence of sexual selection on plumage coloration in a southern Appalachian mountain population of eastern bluebirds. I found that females that were more-ornamented (greater UV-reflectance of structural plumage and darker, more red chromatic breasts) tended to lay eggs earlier in the season and had heavier body mass compared to the less-ornamented females. Among males, there were no significant relationships between color and reproductive success suggesting that females may not assess male plumage coloration. My data suggest that, in this population, female plumage coloration may be driven by sexual selection and could be a signal

of quality to conspecifics. Male mate choice for a high-quality partner or female competition over breeding resources may be driving this selection.

Introduction:

In many species, individuals express elaborate traits used in the acquisition of mates. Like natural selection which acts on the traits that result in the highest fitness, sexual selection acts on traits directly related to mating success (Andersson 1994). Darwin first introduced this concept when trying to explain why males have elaborate and seemly non-adaptive ornamentation as it is costly to produce and highly conspicuous to predators (Darwin 1871). Male-male competition and female choice were proposed as the central mechanisms to explain male ornamentation (Tobias et al. 2012). The benefits of attracting mates leads to higher reproductive success and outweighs the cost of bearing these ornaments and perpetuates them into future generations (Andersson 1994). Females, however, often have subdued traits compared to males and there is debate as to what mechanisms drive their ornamentation. The genetic correlation hypothesis states that female traits are simply byproducts from the selection on male traits; because the two sexes share most of their genome, selection on male traits will drag along expression of elaborate traits in females (Amundsen 2000; Tobias et al. 2012). Alternatively, there may be direct selection acting on female ornamentation through female-female competition or male mate choice (Amundsen 2000; Kraaijeveld et al 2007; Clutton-brock 2009). Among females, coloration may act as a signal of dominance in the competition for breeding resources. Males may also use female ornamentation when selecting mates (Clutton-brock 2009).

Females are often regarded as the choosier sex as females in most species invest more energy into reproduction; egg production and raising young is energetically expensive compared to male investment in sperm (Tobias et al. 2012). However, in species in which males and females provide similar levels of parental care, females may benefit from signaling with ornaments, and males would benefit from being just as choosy as females in mate choice. Traits that influence female choice may also influence male mate choice. In zebra finches (*Taeniopygia guttata*), males prefer to mate with the more fecund females demonstrating that males are able to distinguish between females of variable fecundity and experience the benefits of mate selection (Jones et al. 2001). Mutual mate choice occurs in crested auklets (*Aethia cristatella*); both males and females prefer mates with larger crests (Jones et al. 1993).

Males in many bird species display brightly-colored plumage while females typically are subdued in their color (Hill and McGraw 2006). Plumage coloration in birds is produced by either carotenoid pigments, melanin pigments, or feather microstructure (Hill and McGraw 2006). These three mechanisms involve physiological costs to produce or maintain and therefore can signal individual quality to conspecifics. In species with biparental care, females may also exhibit increased coloration. When male and female birds are similarly ornamented it could suggest sexual selecting acting on females. For example, male bluethroats (*Luscinia svecica*) prefer more colorful females as mates and those females are also in better body condition (Amundsen 1997). In blue tits (*Cyanistes caeruleus*), the ultraviolet coloration of females predicts reproductive success (Henderson et al. 2013). These studies suggest that males should gain fitness benefits from choosing to pair with brightly colored females.

The eastern bluebird is a socially monogamous songbird that exhibits biparental care. They are sexually dichromatic, and females are ornamented but display duller color than males. Males have blue, ultraviolet structural coloration across their head, rump, and tail feathers and melanin-based chestnut breasts. In an Alabama population, male bluebirds that are more-ornamented have higher reproductive success indicating sexual selection (Siefferman and Hill 2003). Males with more ornamentation were also better competitors for high-quality territories (Siefferman and Hill 2005b) and tend to be mated to females that invested more in offspring care

(Ligon and Hill 2010). Contradictory evidence exists as to whether the plumage coloration for female eastern bluebirds is sexually selected. In an Alabama population, Siefferman and Hill (2005a) found that females with more chromatic UV-blue coloration lay eggs earlier in the season, provision offspring at higher rates and achieve higher reproductive success. However, in a Virginia population, blue tail coloration of females was only weakly predictive of reproductive success (Hubbard 2009).

Here, I test the hypothesis that plumage coloration in male and female eastern bluebirds is representative of their individual quality and could therefore be a sexually selected trait. Using a long-term data set, I explore relationships between plumage coloration and 1) female body size and 2) fitness metrics including: breeding onset date, hatching success, and the number of offspring fledged. I predicted that birds with brighter, more ultraviolet reflecting rumps and darker, more red, chromatic breasts (that is, females with more male-like coloration), would commence breeding earlier in the season, experience higher hatching success, rear more offspring to independence, and exhibit higher body mass.

Methods:

I analyzed a dataset from a population of eastern bluebirds in Watauga County, North Carolina (36°11" 39"N, 81°44" 5"W) from 2009 until 2017. These data were collected by Lynn Siefferman and students in her lab who monitor 300 nest boxes from late April until early August. Nest data recorded included: the date the first egg was laid, the number of eggs laid, and the number of nestlings fledged per nest. Hatching success was calculated as the number of fledglings divided by the clutch size. Eastern bluebirds in this population typically have about two broods per season, and thus I also calculated the total number of nestlings that fledged per mated pair per season to quantify reproductive success for each adult. Each year, adult birds were captured and banded with one aluminum U.S.G.S. band and a unique combination of three colored bands used for identification. Upon capture, body mass was measured, and feathers were collected for spectrometric analyses including: nine feathers from the rump and nine from the breast. Across the years, 547 adults were captured (313 females and 234 males).

Plumage Color Analysis

After collection, feathers were stored in envelopes in a climate-controlled environment until spectral analysis. Feathers were taped and arranged onto black paper how they would lay naturally on the bird. Following Siefferman and Hill (2003) the spectral data was recorded using a reflectance spectrometer (range = 250-889 nm; Model S2000, Ocean Optics, Dunedin, FL, USA) equipped with a micron fiber-optic probe placed at a 90° angle to the feather surface. The probe was fixed to read at a 6-mm distance from the feather and recorded a 2-mm diameter area with the use of a deuterium bulb (UV light source) and a tungsten-halogen bulb (visible light source). All data was produced against a white standard (Labsphere, Inc.). For the breast and rump feathers, five spectral measurements were recorded for each region picking up the probe between each measurement and those measures were averaged.

Color was quantified using three standard descriptors of reflectance spectra: brightness, chroma, and hue. Brightness is the total amount of light reflected by the feather and was calculated as the sum of reflectance from 300 to 700 nm. Chroma was calculated differently for the blue and chestnut colored regions on the birds as these two colors have different spectral properties. Chroma is a measure of spectral purity, and for the blue structural coloration of the rump and tail, I calculated ultraviolet (UV) chroma as the ratio of reflectance in the UV part of the spectrum (300-400 nm) to the total amount of reflectance (300-700 nm). Red chroma from the chestnut breast coloration was calculated as the ratio of reflectance in the red part of the spectrum (575-700 nm) to the total amount of reflectance (300-700 nm). Hue is the major color seen reflected by the feather. For the blue structural coloration, I calculated hue as the wavelength at the peak reflectance point. For chestnut breast coloration, I did not include a hue measurement because it was nearly uniform among birds.

Statistical Analyses

I standardized our data by year, as plumage color varied significantly between breeding seasons. Male and female plumage color was also significantly different from one another, so I split the data by sex to analyze the two sexes separately. I used linear mixed models to investigate whether adult plumage coloration was related to adult reproductive success and fitness. In our models, fixed effects included first egg date (Julian date at which a bird laid its first egg of the breeding season), total yearly fledged (number of nestlings fledged from nest throughout entire breeding season), hatching success (number of nestlings that hatched from the first clutch of the breeding season) and mass. All fixed effects were standardized as there was variation from year to year. Our random effect was adult bird band number (ID). The predictor variables were five plumage color variables: breast brightness (BB), breast red chroma (BRC), rump brightness (RB), rump UV chroma (RUVC), and rump hue (RH). I excluded interactions between color variables as these regions are inherently correlated and not the focus of these models. I ran all models with interactions between color variables and mass, but when compared to models excluding interactions, I found no difference in our overall results, so I chose the more parsimonious models excluding these interactions. I used Akaike Information Criterion (AIC) model fitting to explore how well models explained our data (Burnham and Anderson 2002). Models that did not differ by >2 AIC points were considered equal. As many models resulted in inconclusive results, I used variable importance and coefficients from a model including each variable to help us in selecting the most likely models (Burnham and Anderson 2002).

All statistics were conducted using R version 3.4.3. Linear mixed models were created using the R packages lme4 and lmerTest. The MuMln package was used to average models and determine model likelihood.

Results:

First Egg Date

It was not possible to distinguish the best model for explaining first egg date in females as the delta AIC values are extremely close between models and the weights (W_i) are relatively weak (Table 1). Ranking the variables by their importance within the set of models suggests that the best model would most likely include rump UV chroma, breast red chroma, and breast brightness as these three variables hold the most weight within the models (RUVC = 95.1%, BRC = 60.5%, BB = 59.4%; Table 9). As a pair, rump UV chroma and breast red chroma occurred in the models together 57.0% of the time, and rump UV chroma and breast brightness occurred 56.7% of the time. All three top predictor variables show up together 26.1% of the time. Rump UV chroma had the largest coefficient and was a significant predictor when in a model including all variables ($p = 0.0153$) suggesting it is the most important predictor variable for first egg date in females. Using a linear regression, rump UV chroma was significant in predicting first egg date in females (Figure 1; Adj. $R^2 = 0.05252$, $F_{(1,311)} = 18.3$, $p < 0.0001$). The most likely model then for explaining first egg date in females includes either rump UV chroma and breast red chroma or rump UV chroma and breast brightness, but it does not likely include all three. Model selection suggested that females that laid eggs earlier in the season tended to have blue structural plumage with greater UV chroma, and chestnut breast coloration with greater red chroma and darker coloration, thus they tend to be females with more ornamented (or more male-like) plumage (Table 1).

No model best explained the date that the males mate laid the first egg as the delta AIC values were extremely close and the weights (W_i) are relatively weak (Table 2). Breast brightness and rump hue hold the largest weight within the models (BB = 57.2%, RH = 57.5%; Table 10). Rump hue had the largest coefficient when in a model containing all color variables, but it was not significant (p=0.0614). The best fitting model would most likely include rump hue and breast brightness as predictors. Thus, in males, coloration is not a good predictor of their mate's egg laying dates.

Total Yearly Fledged

There was evidence, although weak, that the null model was the best fitting model to explain total offspring fledged for females as the weight of the null model was relatively large (Table 3). The next best models (using delta AIC values) included red chroma of breast and UV chroma of rump though these models have slightly lower weights. Variable importance suggested that brightness of rump carried the most weight in the models (RB = 64%; Table 9), and, in a model including all variables, it also had the largest coefficient though it was not significant (p = 0.0876). These results suggest that females that fledge more offspring during the breeding season tended to show a weak tendency to have lighter chestnut (more female-like) breast plumage (Table 3). There was also a weak trend such that females with duller (more female-like) blue structural plumage fledged more offspring during the breeding season (Table 3).

The first three suggested models for total offspring fledged for males were indistinguishable in their importance as their delta AIC values are close and their weights were approximately equal (Table 4). Variable important showed that UV chroma of rump and rump brightness were about equal in weight among models (RUVC = 43.5%, RB = 42.0%; Table 10). As a pair, they only weighed 14.1% in the models which is roughly the same weight of the null model (null model W_i = 11.2%). The null model, a model including just rump UV chroma, or a model including just rump brightness were the most likely models. Rump UV chroma had the largest coefficient when in a model including all variables, though no variable present significantly predicts total offspring fledged in males. Thus, male coloration was not a good predictor of the total amount of offspring fledged by his mate in the breeding season.

Hatching Success

There was evidence, although weak, that the null model was the best fitting model to explain hatching success for females as the model weight was relatively large (Table 5). Variable importance showed that rump hue had the most impact within the possible models on hatching success for females (RH = 49.0 %; Table 9). Rump hue had the largest coefficient in a model including all color variables, though it was not significant ($p = 0.0837$). This points to females with greater hatching success exhibiting more longer-wavelength hues in their blue structural plumage, thus they were females that are less ornamented (more female-like).

A likely model for explaining hatching success in males included rump brightness as a predictor as it has the lowest AIC value and the highest weight of the models (Table 6). Rump brightness had the highest weight in terms of variable importance (66.8%; Table 10). In a model including all variables, rump brightness had the largest coefficient, though it was not significant (p=0.0908). These results suggest that males that were mated with females that had higher hatching success tended to have brighter blue structural plumage.

Mass

There was evidence in support of the 1st model in predicting mass of females as the delta AIC between it and the next model was relatively large and the weight was large in comparison to the rest of the models ($W_i = 19.7\%$). Rump UV chroma had the highest variable importance followed by breast brightness (RUVC = 95.9%, BB = 65.1%; Table 9). As a pair, rump UV chroma and breast brightness occurred in the models 62.3% of the time. Rump UV chroma had the largest coefficient and was most significant in predicting mass in the model including all variables ($p = 0.0133$). Breast brightness had a similarly large coefficient and was also significant in predicting mass in a model including all variables ($p = 0.0473$). Using a linear regression, rump UV chroma was a significant predictor of mass (Figure 2; Adj. $R^2 = 0.04123$, $F_{(1,311)} = 14.43$, $p < 0.0001$). Rump UV chroma and breast brightness were likely included in the best model. This suggests that females that were heavier tended to have blue structural plumage with greater UV chroma and darker breasts, thus they were more ornamented (more male-like).

There was support that the null model was the most likely model in explaining mass of males as the delta AIC between it and the next model were relatively large and the weight was large in comparison to the other models (Table 8). All variables were relatively similar in weight within the possible models (Table 10). In a model including all variables, breast brightness had the largest coefficient though it was not significant ($p = 0.514$). Thus, male coloration was not a good predictor of body mass.

Discussion:

In this study, I found evidence that sexual selection may be acting on female plumage color in a population of eastern bluebirds in the Southern Appalachians. In this population, more-ornamented females laid eggs earlier in the breeding season and were heavier than less-ornamented females. This suggests that plumage coloration in females is related to individual quality and has the potential to signal useful information to conspecifics possibly through male mate choice or female-female competitive interactions. Unlike a population in Alabama, I found no evidence of a relationship between male plumage coloration and reproductive parameters suggesting no evidence of sexual selection currently acting on male plumage color in this Southern Appalachian population.

First egg laying date can be a good representation of individual quality because depending on the level of physiological condition, a bird may be limited on when they can begin raising offspring. A bird who initiates egg laying sooner is likely an individual of higher-quality as the earlier a bird can begin may dictate how many successful nesting opportunities they can achieve in the breeding season; earlier egg laying dates set up the potential for a greater number of total offspring fledged. The eastern bluebird is an obligate secondary cavity nester, and the availability of nesting cavities is a limiting resource for breeding bluebird pairs. As eastern bluebirds exhibit bi-parental care with the male helping provision nestlings, both the male and female actively defend their territory throughout the breeding season. Actively defending a territory is energetically demanding, so it would take the highest quality individuals to be able to both secure and defend nest boxes (Ligon 1999). Females in this study that exhibited greater ornamentation laid eggs earlier in the season (Figure 1). The relationship between female plumage color and first egg date in this population suggest that color can be a good predictor of individual quality in the early stages of breeding. Females that are more-ornamented may be using their color as a signal to mediate competitive interactions among other females for nest boxes or in male mate choice.

It is interesting that in this study females that were more-ornamented laid eggs sooner but did not necessarily produce a greater number of offspring in comparison to less-ornamented females. This relationship may be a product of trade-offs between ornamentation and reproduction or that the eastern bluebirds in this Southern Appalachian population deal with stochastic factors that can impact if a nesting attempt is successful; unforeseen predation and weather can fail an early nest by a high-quality female. Breeding early is risky; in the Southern Appalachians, early season cold snaps can lead to nest failure. The patterns in this dataset could have been clearer if we had been able to capture early season nesters before nest failure.

Females in this population that were more-ornamented had a heavier mass than less-ornamented females (Figure 2). This suggests that female plumage color has the potential to signal individual quality to conspecifics. The handicap hypothesis explains that higher quality individuals can more easily afford to display elaborate secondary sexual characteristics as these traits are expensive to develop, grow, and maintain (Zahavi 1975). Multiple lines of evidence from the Alabama population suggests that blue structural coloration in female bluebirds is condition dependent; female blue structural color is dependent on nutrition (Siefferman and Hill 2005a), and the blue color in both sexes is positively affected by wetter and cooler weather during molt likely of the positive effects on arthropod abundance (Warnock 2017). Individual quality is often measured using body mass as the energy demands for the production and maintenance of color are high; if an individual can both display a greater degree of ornamentation and have a larger mass than conspecifics, then it indicates the better body condition of that bird (Siefferman and Hill 2005a; McGraw 2007). There are advantages for males and females to choose a high-quality mate as these individuals may provide numerous benefits including resources within a territory and good genes (Andersson 1994).

There is no evidence that sexual selection is currently maintaining elaborate plumage coloration of male eastern bluebirds in the Southern Appalachians; my data revealed no significant relationships between plumage color and reproductive parameters. Brighter males were not mated to females that laid eggs earlier and color did not predict total reproductive output. Further, I found no significant relationships between color and body mass in males. Together, there is no evidence that plumage has the potential to signal individual quality. These patterns differ from those of an Alabama population, where males that are more-ornamented experience greater reproductive success (Siefferman and Hill 2003). These differing patterns of plumage color and reproductive parameters in the Southern Appalachian and Alabama populations suggest geographic variation in the strength of sexual selection occurring. There are other avian species wherein patterns of sexual selection vary geographically. In barn swallows (*Hirundo rustica*), the traits that are currently driven by sexual selection (outer tail length, breast coloration) vary geographically (Romano et al 2016). Further, female common yellowthroats (*Geothylpis trichas*) in two different populations prefer different ornaments and, in each population, the male traits under selection reliably indicate male quality (Whittingham et al 2015). In a Wisconsin population, female common yellowthroats prefer males with larger black masks while females in New York chose mates based on bib size (Dunn et al 2008). Indeed, there is geographic variation in plumage coloration in eastern bluebirds; birds in the more southern extent of their breeding range are more colorful (Warnock 2017). Environmental factors, how signals are perceived or strength of females’ preferences may be differently affecting regional sexual selection for traits. Alternatively, the lack of relationships between male quality and color in this study may be because our sample size for males was smaller than that of females. It is easier to capture females than males during the incubation stage. As nest boxes are a limiting resource for cavity nesting birds, we may have an over saturated field site given that we have 300 nest boxes, and many are often unused. A study that limits cavity availability may allow researchers to better see trends associated with intra-sexual competition.

There is some evidence that suggest that males may be paying attention to female plumage color in this population. Males show favoritism to sons over daughters in this population only when they are mated to more colorful females (Barrios-Miller 2013). In a Virginia population, males did not seem to prefer colorful females (Hubbard 2009). Female birds may paying attention to female coloration and could use it to gauge competitive ability when competing over nest boxes. In female blue tits, their UV-reflecting crown ornamentation affected the female’s reaction towards female intruders (Midamegbe et al 2011). In this NC bluebird population, the more-ornamented females laid eggs earlier suggesting selection for highly-ornamented females may be driven by female-female competition for nest boxes early in the season. Melanin-based pigmentation and microstructures forming structural plumage in feathers are known to be expensive to produce and maintain, thus they can be honest signals of quality (Hill and McGraw 2006). In the Kentucky warbler (*Geothlypis formosa*), melanin-pigmented ornaments can signal condition and explain variation in mating success (Parker et al 2003).

Although male eastern bluebirds are more colorful than females, evidence of sexual selection in females exists from three different populations including this study (Siefferman and Hill 2003, 2005a; Hubbard 2009); highly-ornamented females from both Alabama and Virginia populations experienced greater reproductive success. In the Alabama population, male ornamentation predicted their competitive ability, and males view territorial intruding males as threats when they are more-ornamented (Siefferman and Hill 2005b; Mercadante 2014). The role of female color in mediating female-female interactions has not yet been studied in bluebirds but such research would help understand the mechanisms of sexual selection driving more-ornamented females to lay eggs earlier. In this Southern Appalachian population, bluebirds are not only competing among conspecifics for nest boxes, but they are also dealing with pressure from tree swallows (*Tachycineta bicolor*) undergoing a southward range expansion into the bluebirds' range. Aggression in female secondary cavity nesters is an important trait that may determine if securing a nest box is successful. In the pied flycatcher (*Ficedula hypoleuca*), forehead patch signals fighting ability in males as well as playing a role in intrasexual competition between females (Morales et al 2014).

The results from this study point to sexual selection acting on the plumage color of female eastern bluebirds. As the mechanisms for this to act are still unclear, studies should look at the relationship between female aggression and competitive ability as it relates to plumage color to determine if competition over resources is driving selection for more-ornamented females. Female aggression as a sexually selected trait is not well represented in the literature but the few studies looking at this have produced interesting results; female tree swallows that successfully obtained nest boxes were significantly more aggressive than females that did not, suggesting the importance of this trait in female-female competitive interactions (Rosvall 2008). Due to their obligate cavity nesting life style, eastern bluebird populations are easily studied, and thus future research should focus on a more comprehensive approach to understanding patterns of geographic variation in sexual selection and the drivers behind these patterns.

References:

Amundsen, T., E. Forsgren, and L. T. T. Hansen. 1997. On the function of female ornaments: male bluethroats prefer colourful females. Proc. R. Soc. Lond. B 264:1579–1586.

Amundsen, Trond. 2000. Female Ornaments: Genetically Correlated or Sexually Selected? Animal signals: Signalling and signal design in animal communication. 133-154.

Andersson M, 1994. Sexual Selection. Princeton: Princeton University Press.

Barrios-Miller, N. L., & Siefferman, L. 2013. Evidence that fathers, but not mothers, respond to mate and offspring coloration by favouring high-quality offspring. *Animal behaviour*, *85*(6), 1377-1383.

Clutton-Brock, T. 2009. Sexual selection in females. *Animal Behaviour* 77.1: 3-11.

Darwin, C. 1871. The descent of man and selection in relation to sex. Murray, London.

Henderson, L. & Heidinger, B. & Evans, N. & Arnold, K. 2013. Ultraviolet crown coloration in female Blue Tits predicts reproductive success and baseline corticosterone. *Behavioral Ecology*. 24.

Hill, G. E., and K. J. McGraw. 2006. Preface. In G. E. Hill and K. J. McGraw, eds. Bird coloration. Vol I. Harvard Univ. Press, Cambridge, MA. In press.

Hubbard, J. 2009. Female Plumage Coloration in Eastern Bluebirds, Sialia sialis: Is it a Sexually Selected Trait? Masters's Thesis. College of William and Mary, Virginia.

Jones, I. L., & Hunter, F. M. 1993. Mutual sexual selection in a monogamous seabird. *Nature*, *362*(6417), 238.

Jones K., Monaghan P., Nager R.. 2001. Male mate choice and female fecundity in zebra finches. *Animal Behaviour*. 62:1021-1026.

Kraaijeveld, K., Kraaijeveld-Smit, F. J., & Komdeur, J. 2007. The evolution of mutual ornamentation. *Animal Behaviour*, *74*(4), 657-677.

Ligon, J. D. 1999. The Evolution of Avian Breeding Systems. Oxford: Oxford University Press.

Ligon, R., & G. Hill. 2010. Sex-Biased Parental Investment Is Correlated with Mate Ornamentation in Eastern Bluebirds. *Animal behaviour* 79.3 (2010): 727–734.

Mercadante, A. & Hill, G. 2014. An experimental test of the role of structural blue and melanin-based chestnut coloration in aggressive contests in male eastern bluebirds. *Frontiers in Ecology and Evolution.* 2.

Midamegbe, A. & Grégoire, A. & Perret, P. & Doutrelant, C. 2011. Female–female aggressiveness is influenced by female coloration in Blue Tits. *Animal Behaviour*. 82. 245-253.

Siefferman L, Hill GE, 2003. Structural and melanin coloration indicate parental effort and reproductive success in male eastern bluebirds. Behavioral Ecology 14:855-861.

Siefferman L, Hill GE, 2005a. Evidence for sexual selection on structural plumage coloration in female eastern bluebirds (Sialia sialis). Evolution 59:1819-1828.

Siefferman L, Hill GE, 2005b. UV-blue structural coloration and competition for nestboxes in male eastern bluebirds. Animal Behaviour 69:67-72.

Tobias, J. A., Montgomerie, R., & Lyon, B. E. 2012. The evolution of female ornaments and weaponry: social selection, sexual selection and ecological competition. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1600), 2274–2293.

Rosvall, K. A. 2008. Sexual selection on aggressiveness in females: evidence from an experimental test with tree swallows. *Animal Behaviour*, *75*(5), 1603-1610.

Warnock, MC. 2017. Variation in plumage coloration of eastern bluebird (Sialia sialis) in relation to weather and geography. Master's Thesis. Appalachian State University, Boone, NC.

Zahavi, A. 1975. Mate selection: a selection for a handicap. J. *Theor*. *Biol*. 53:205–214.

Acknowledgments

I am grateful to my advisor Dr. Lynn Siefferman for her endless guidance and support throughout the challenges of this project. She pushed me to be curious and passionate about research and has inspired me to be confident in my future scientific endeavors. I am thankful to Dr. Michael Osbourn for his feedback on my thesis drafts, Dr. Daniel Becker from Montana State University for his long-distance statistical support in R, Tyler Pyle for his help with statistics and his mentorship in the lab, and the Siefferman-Gangloff lab for their data collection that made this project possible and their kindness throughout my time in the lab. Lastly, I thank my ever-encouraging parents for always reassuring me and rooting for me and Alex for his unfailing love and emotional support.

Tables and Figures:

Figure 1: The relationship between first egg date (FED) and rump UV chroma in female eastern bluebirds (n = 313, Adj. $R^2 = 0.05252$, $p < 0.001$).

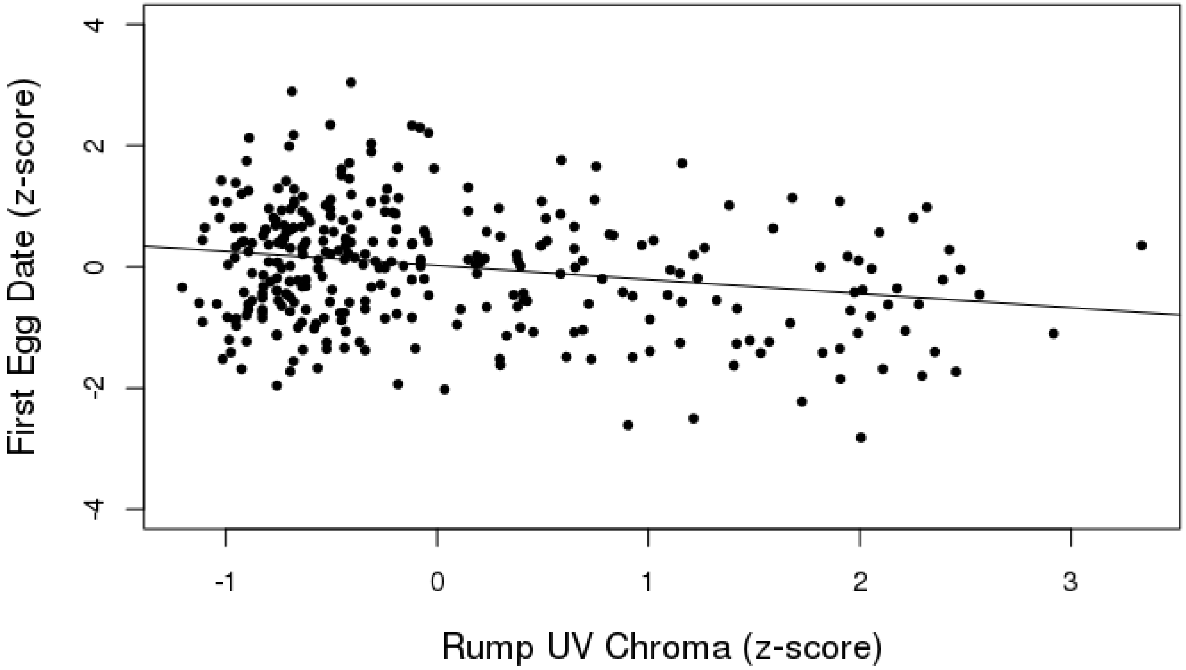

Figure 2: The relationship between mass and rump UV chroma in female eastern bluebirds (n = 313, Adj. R2 = 0.04123, $p < 0.001$).

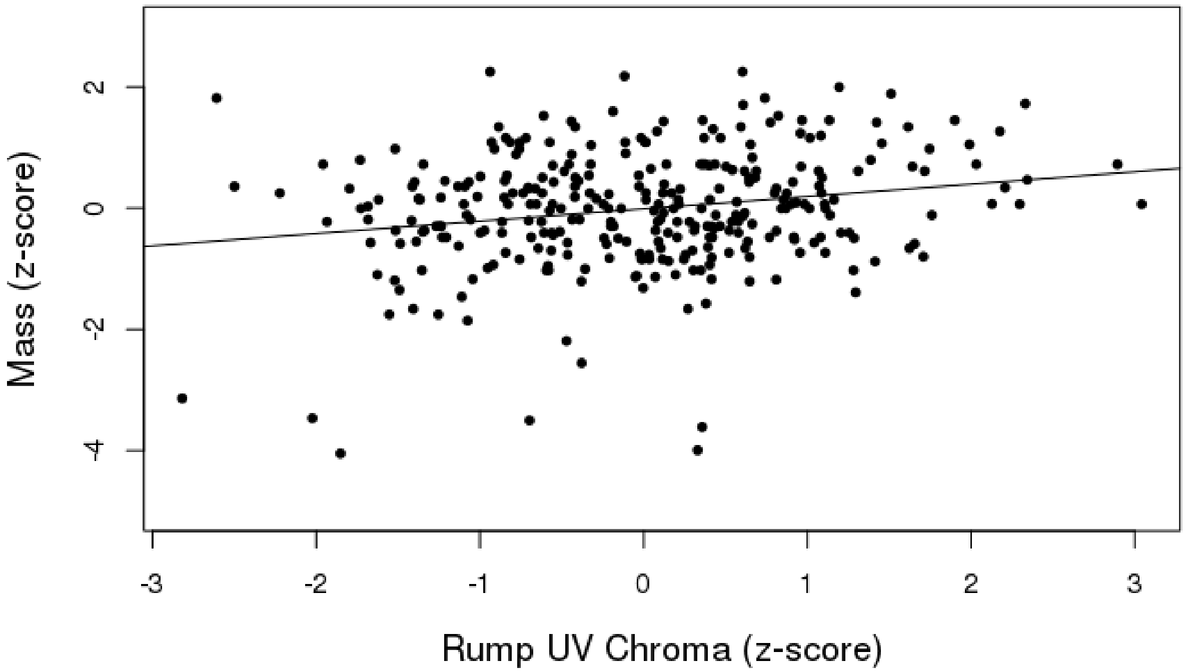

Table 1: Model selection for plumage color variables predicting first egg date (FED) in female eastern bluebirds.

Model	**Δ AIC$_c$**	**W$_i$**	**R^2**
BRC + RUVC	0.00	0.131	0.306
BB + RUVC	0.11	0.124	0.367
BB + BRC +RUVC	0.36	0.110	0.324
BB + RH + RUVC	0.54	0.100	0.384
BRC + RH + RUVC	0.76	0.090	0.320
BB + BRC + RH + RUVC	0.96	0.081	0.341
BRC + RB + RUVC	1.84	0.052	0.315
BB + RB + RUVC	2.11	0.046	0.371
BB + BRC + RB + RUVC	2.36	0.040	0.329
BB + RB + RH + RUVC	2.56	0.037	0.388

Table 2: Model selection for plumage color variables predicting first egg date (FED) in male eastern bluebirds.

Model	**Δ AIC$_c$**	**W$_i$**	**R^2**
BB	0.00	0.075	0.181
BRC + RH + RUVC	0.22	0.068	0.175
BB + RH	0.32	0.064	0.202
BB + RH + RUVC	0.39	0.062	0.202
BRC + RH	0.50	0.059	0.177
BRC	0.52	0.058	0.156
BB + BRC	0.80	0.051	0.165
BB + BRC + RH	0.90	0.048	0.185
BB + BRC + RH + RUVC	1.04	0.045	0.184
BB + RB + RH	1.58	0.034	0.212

Table 3: Model selection for plumage color variables predicting total yearly fledged (TYF) in female eastern bluebirds.

Model	**Δ AIC$_c$**	**W$_i$**	**R^2**
Null	0.00	0.123	0.113
RB + RUVC	0.77	0.083	0.143
RB	1.14	0.069	0.120
RUVC	1.20	0.067	0.122
RH	1.56	0.056	0.113
BB	1.57	0.044	0.115
BB + RB + RUVC	2.03	0.044	0.148
BRC	2.04	0.041	0.112
RB + RH	2.20	0.035	0.122
BB + RB	2.48	0.030	0.124

Table 4: Model selection for plumage color variables predicting total yearly fledged (TYF) in male eastern bluebirds.

Model	**Δ AIC$_c$**	**W$_i$**	**R^2**
RUVC	0.00	0.113	0.061
Null	0.02	0.112	0.013
RB	0.16	0.105	0.048
RB + RUVC	1.49	0.054	0.070
RH + RUVC	1.78	0.047	0.070
BB + RB	1.91	0.044	0.048
BRC	1.97	0.042	0.020
BB	1.99	0.042	0.011
BRC + RB	2.00	0.042	0.059
BRC + RUVC	2.04	0.041	0.066

Table 5: Model selection for plumage color variables predicting hatching success (HS) in female eastern bluebirds.

Model	**Δ AIC_c**	**W_i**	**R^2**
Null	0.00	0.125	0.815
RH	0.89	0.080	0.816
RH RUVC	1.04	0.074	0.825
RB	1.42	0.061	0.815
BRC	1.54	0.058	0.803
RB + RH	1.55	0.057	0.819
RUVC	1.82	0.050	0.817
BB	2.04	0.045	0.813
BRC + RH	2.28	0.040	0.803
RB + RH + RUVC	2.54	0.035	0.825

Table 6: Model selection for plumage color variables predicting hatching success (HS) in male eastern bluebirds.

Model	**Δ AIC_c**	**W_i**	**R^2**
RB	0.00	0.160	0.045
RB + RH	1.10	0.092	0.058
BRC + RB	1.83	0.064	0.043
BB + RB	1.88	0.062	0.053
Null	2.08	0.056	0.045
RB + RUVC	2.09	0.056	0.046
RH	2.50	0.046	0.063
BRC + RB + RH	2.86	0.038	0.056
RB + RH + RUVC	2.91	0.037	0.061
BB + RB + RH	2.97	0.036	0.066

Table 7: Model selection for plumage color variables predicting mass in female eastern bluebirds.

Model	Δ AIC_c	W_i	R^2
BB + RUVC	0.00	0.197	0.474
RUVC	0.97	0.121	0.445
BB + BRC + RUVC	1.16	0.110	0.446
BB + RH + RUVC	1.42	0.097	0.476
BB + RB + RUVC	2.04	0.071	0.474
RH + RUVC	2.49	0.057	0.444
BB + BRC + RH + RUVC	2.55	0.055	0.467
RB + RUVC	2.83	0.048	0.449
BRC + RUVC	3.03	0.043	0.442
BB + BRC + RB + RUVC	3.24	0.039	0.465

Table 8: Model selection for plumage color variables predicting mass in male eastern bluebirds

Model	Δ AIC_c	W_i	R^2
Null	0.00	0.182	0.294
BB	1.18	0.101	0.291
BRC	1.78	0.075	0.275
RUVC	1.94	0.069	0.290
RB	2.03	0.066	0.287
RH	2.07	0.065	0.294
BB + RUVC	3.20	0.037	0.289
BB + BRC	3.25	0.036	0.285
BB + RB	3.27	0.028	0.288
BB + RH	3.27	0.027	0.282

Table 9: Variable Importance of plumage color variables within female models

	Female Model Selection Tables			
Plumage Color Variables	Table 1: FED	Table 3: TYF	Table 5: HS	Table 7: Mass
RB	27.9 %	64.0 %	34.5 %	27.3 %
RUVC	95.1 %	40.6 %	35.2 %	95.9 %
RH	45.3 %	30.4 %	49.0 %	35.0 %
BB	59.4 %	32.9 %	26.5 %	65.1 %
BRC	60.5 %	24.7 %	31.5 %	32.0 %

Table 10: Variable Importance of plumage color variables within male models

	Male Model Selection Tables			
Plumage Color Variables	Table 2: FED	Table 4: TYF	Table 6: HS	Table 8: Mass
RB	26.1 %	42.0 %	66.8 %	26.7 %
RUVC	41.1 %	43.5 %	29.4 %	27.7 %
RH	57.5 %	27.4 %	38.9 %	26.2 %
BB	57.2 %	27.1 %	29.1 %	33.9 %
BRC	53.0 %	27.1 %	29.0 %	28.1 %