

**Condition Dependence and Status Signaling Function of Structural Coloration in
the Eastern Bluebird (*Sialia sialis*)**

by

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Abstract

I examined the relationship between blue feather coloration, nutritional condition, and status signaling in eastern bluebirds (*Sialia sialis*). I quantified nutritional condition by measuring growth rates of tail feathers for an entire bluebird population to compare different age classes for both males and females. I found that males had wider growth bars than females and that older breeders had wider growth bars than younger breeders. Wider growth bars were correlated with longer tail feathers. Growth bar width was correlated with tail coloration for yearling males but not for males older than two years. Growth bar width was correlated with tail coloration in all females but there was a stronger correlation for second year females. Growth bar width was significantly correlated with number of offspring fledged the prior year as well as the number of offspring produced in the current year. I then compared the behavioral response from territorial males toward artificially brightened and darkened model conspecifics to test the signaling function of bright plumage. Bluebird males attacked models with brighter blue coloration significantly more often than models with darker blue coloration. Bluebird males did not attack models with brighter chestnut coloration significantly more often than models with darker chestnut coloration. The structurally-based blue plumage appears to be condition dependent and a signal of status used during male competition, whereas the melanin-based orange plumage does not.

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CHAPTER ONE

Condition Dependence of Structural Coloration in the Eastern Bluebird

ABSTRACT

Elaborate plumage, whether used for intrasexual or intersexual selection, must be difficult to acquire or retain in order to be an honest signal of status. However, the relationship between structurally produced blue feather coloration and an individual's nutritional condition is unclear. I examined the relationship between blue feather coloration and nutritional condition at time of molt in eastern bluebirds (*Sialia sialis*) by measuring growth rates of tail feathers of an entire bluebird population. I measured growth bars on tail feathers of males and females of different age classes and compared growth bar width to age, gender, tail feather chroma, and number of offspring produced. I found that males had wider growth bars than females and older birds had wider growth bars than first time breeders. Wider growth bars were correlated with longer tail feathers. Growth bar width was correlated with tail coloration in yearling males but not males older than two years. Growth bar width was correlated with tail coloration in all females, but there was a stronger correlation for second year females. Growth bar width was significantly correlated with number of offspring fledged the prior year as well as the number of offspring fledged the current year. The structurally-based blue plumage in eastern bluebirds appears dependent upon condition at time of molt.

INTRODUCTION

Honest indicators of individual condition must be difficult to produce or maintain (Zahavi 1975) so that cheating does not diminish the reliability of the status signal. Elaborate plumage, whether used for intrasexual or intersexual selection, can serve as an honest indicator of individual condition if it is limited by the nutrients required to develop the ornament or the time needed to consume the necessary amount of nutrients. Several types of ornamental plumage pigments have been found to be either difficult to acquire (e.g. carotenoids (Hill and Montgomerie 1994)) or difficult to maintain in a social group (e.g. melanins (McGraw et al. 2003)) due to repeated challenges from conspecifics. However, whether blue structural coloration is condition dependent trait is a matter of ongoing debate.

Non-iridescent structural coloration in feathers is the result of coherent scattering of light in a keratin-air matrix in the spongy medullary layer of the feather (Prum 2006). Prum et al. (2009) said that the structures in the keratin matrix creating the blue coloration are self-assembling and are not nutrient limited or dependent upon the condition of the individual. However, empirical evidence supports at least partial condition dependence of blue feather coloration. Shawkey et al. (2003) found that the number and similarity of the microstructure keratin rods correlated with the chroma and saturation of a feather with structural coloration. Furthermore, the thickness of the keratin cortex layer, which can affect the total amount of reflected light, may be affected by feather degrading bacteria (Shawkey et al. 2007; Gunderson et al. 2009). At least one study to date has attempted to indirectly link condition and coloration in eastern bluebirds (*Sialia sialis*). Bluebirds that were randomly given increased broods and therefore forced

to devote increased parental effort in one season had decreased coloration in following years (Siefferman and Hill 2005), presumably due to being in poorer condition during the molt at the end of the breeding season.

I examined the relationship between blue structural coloration and nutritional condition at the time of molt in eastern bluebirds by measuring tail feather growth rates. Feathers grow at different rates during a day leaving light and dark bands (called growth bars) that represent corresponding periods of fast and slow growth (Michener and Michener 1938; Wood 1950; Brodin 1993). Feather growth rates (ptilochronology) as a measure of avian condition have increasingly been used in recent decades (Grubb 1989). Growth bar width can be used as a measure of condition at the time of natural molt or as a measure of current condition of a bird by forcing anabolic re-growth after plucking a feather (e.g. Grubb and Yosef 1994) with wider growth bars (i.e. faster feather growth) indicating better condition. Birds may be especially vulnerable to predation during molt (Swaddle and Witter 1997) and thermoregulation may be more difficult during heavy molt, therefore faster feather growth and shorter molt duration should be beneficial.

Feather growth rates have thus far been compared to structural coloration in males of only two species. Keyser and Hill (1999) found that tail feather growth rate was correlated with a score of rump and breast blueness on male blue grosbeaks (*Guiraca caerulea*). Doucet (2002) found that male rump and wing covert coloration related to growth bar width in male blue-black grassquits (*Volatinia jacarina*). However, both studies compare growth bars on one part of the body (tail feathers) to ornamental coloration on another part of the body. There may be a difference of up to several weeks from when individual tail feathers are molted to when specific contour feathers are

molted and so comparing growth rates of one feather patch to coloration on another color patch may not accurately represent the relationship between color and condition at the time of molt of either.

The eastern bluebird is a sexually dichromatic passerine with both structural- and melanin-based ornamental plumage. Males have vivid ultraviolet-blue heads, wings, backs, and tails and a chestnut-orange breast. Females resemble males in patterning but with duller wings, backs, and tails and a fainter breast color. In eastern bluebirds, coloration is related to age (Siefferman et al. 2005) and reproductive success (Siefferman and Hill 2003), and coloration may be a signal used in sexual selection. Although female bluebirds are more dully colored than males, they have bright blue coloration on their wing and tail feathers which may be a sexually selected trait for females as well as for males (Siefferman and Hill 2005). The bluebird's ornamental tail coloration allows us to directly compare a structurally-based ornament with the individual's condition at the time the feather was grown, rather than to another plumage patch which may have grown at a different time from the measured tail feather. Bluebirds do not have a pre-alternate molt and are non-migratory at the study location (Auburn, AL). Brighter individuals are able to breed earlier in the year (Siefferman and Hill 2003), which can lead to more offspring produced in a year (Darwin 1871; Fisher 1930). However, there has not yet been a bluebird study quantifying individual condition at time of molt with the brightness of the feathers produced. I compared growth bars on the outermost rectrices of both male and female eastern bluebirds to color data collected from those feathers and reproductive output over the breeding season to determine if condition at time of molt relates to age, sex, color of an ornamental feather, and reproductive success.

METHODS

I conducted this study in fields adjacent to the Auburn University campus, in Lee County, Alabama (32°35'N, 82°28'W) during spring and summer of 2008, 2009, and 2010 (March – July). I captured breeding males and females at nest boxes using traps and mistnets. All adults were banded with a U.S. Fish and Wildlife Service aluminum band and given three plastic color bands for future identification. Captured bluebirds were weighed with a digital scale accurate to 0.1 g (Flipscale F2), wing length and tail length were measured using a wing ruler accurate to 0.5 mm (Avinet), and bill and tarsus length were measured using calipers accurate to 0.02 mm. Nestlings were banded with only an aluminum band. The Auburn population of breeding bluebirds has been monitored since 1999 so the age of almost all breeding adults is known.

Juvenile eastern bluebirds have an incomplete first pre-basic molt where they replace their juvenile body feathers but retain many of their flight feathers through their second year. Eastern bluebirds have no pre-alternate molt; therefore first time breeders (termed “second year” adults) will often have tail feathers that were grown as nestlings the prior year. At the end of the breeding season (and for all subsequent years), adults have a complete pre-basic molt and will have fully adult plumage the following year (when they will be termed “after second year” adults). Birds of unknown age were included as part of the overall male and female population data but were removed for age-specific analyses.

I captured adult bluebirds and pulled the outermost rectrix (R6) from both sides. I then taped the tail feathers flat on non-reflective black paper (Canson Mi-Tientes, Stygian

Black) and recorded color data with an Ocean Optics S2000 spectrometer (Dunedin, Florida). Following methods described by Siefferman and Hill (2003), I recorded feather reflectance data from 300-700 nm using a micron fiber-optic probe held at a 90-degree incident angle, scanning each feather three times, lifting the probe off the feather between scans. I reduced reflectance data into one color variable: chroma. I define chroma as the proportion of reflectance from 350 to 450 nm (encompassing the entire blue peak) in the total reflectance from 300 to 700 nm. I only use chroma in order to reduce the number of correlations tested and because chroma appeared to be the color variable with the greatest potential to be condition dependent. Hue (the wavelength of maximum reflectance) does not vary greatly in the population (Shawkey et al. 2003), brightness (total reflectance from 300 to 700 nm) seems more likely than chroma to be influenced by external factors (e.g. keratinophilic bacteria degrading the cortex layer (Gunderson et al. 2009)), and chroma appeared to best measure the development of the structures giving the feather its blue coloration (Shawkey et al. 2003). Chroma was standardized to a mean of zero and standard deviation of one for each year to allow for comparisons over multiple years. To determine the growth rate of the rectrices, I counted eight growth bars in the middle third of the feather and pushed pins through the feather vain next to the rachis to mark the width of the eight growth bars. I then measured the distance between the two holes on the back side of the paper using digital calipers accurate to the nearest 0.02 mm and divided the distance measured by the number of growth bars counted (eight) to reach an average growth bar width for each individual.

I compared growth bar width of males and females using a two tailed t-test. I also compared second year birds to after second year birds for each gender using two tailed t-

tests. I then compared growth bar width to chroma of the tail feathers and number of offspring produced. I used a Pearson correlation to compare growth bar width, tail coloration, and reproductive output. Data were analyzed using SAS version 9.1.

RESULTS

Male growth bars were significantly wider than female growth bars ($t = 4.15$, $P = 0.0004$). Male growth bars averaged 3.14 ± 0.01 mm (mean \pm SE) ($n = 234$) and female growth bars averaged 3.08 ± 0.01 mm ($n = 249$). After second year birds had significantly wider growth bars than second year birds for both males ($t = -3.55$, $P < 0.001$) and females ($t = 4.34$, $P < 0.001$).

Growth bar width was significantly positively correlated with the overall length of the tail feather for both males ($r = 0.4$, $P = 0.001$, $n = 234$, Fig 1) and females ($r = 0.39$, $P < 0.0001$, $n = 249$, Fig 2). However, there was no significant correlation between growth bar width and tarsus length for either males ($r = 0.04$, $P = 0.54$, $n = 234$) or females ($r = 0.001$, $P = 0.98$, $n = 249$).

Including all males, there was no significant correlation between growth bar width and tail coloration ($r = 0.12$, $P = 0.27$, $n = 234$, Fig 3A), however there was a significant correlation for second year males ($r = 0.29$, $P = 0.05$, $n = 47$, Fig 3B) while there was no significant correlation for after second year males ($r = -0.05$, $P = 0.58$, $n = 121$, Fig 3C). Female tail coloration was significantly correlated with growth bar width ($r = 0.30$, $P < 0.0001$, $n = 249$, Fig 4A), and second year females had a stronger correlation ($r = 0.35$, $P = 0.02$, $n = 47$, Fig 4B) than after second year females ($r = 0.14$, $P = 0.05$, $n = 119$, Fig 4C).

Male growth bar width was significantly correlated with number of offspring fledged in that year ($r = 0.29$, $P = 0.0005$, $n = 155$, Fig 5A) and the number of offspring fledged in prior years ($r = 0.31$, $P = 0.04$, $n = 37$, Fig 5B). Female growth bar width was correlated with number of offspring fledged in the current year ($r = 0.17$, $P = 0.017$, $n = 174$, Fig 6A) and the prior year ($r = 0.32$, $P = 0.049$, $n = 39$, Fig 6B).

DISCUSSION

For eastern bluebirds, the relationship between feather growth, coloration, and reproductive success depends upon an individual's gender and age. Surprisingly, females exhibited a stronger relationship between tail feather chroma and tail feather growth rate than did males. Both males and females showed a significant correlation between growth bar width and tail length, indicating that there is a structural consequence to the different growth bar widths in the population. However, growth bar width is unrelated to tarsus length, so faster tail growth rate is not simply a byproduct of having a larger body.

For both males and females, second year birds (first-time breeders) had narrower growth bars than after second year birds. This likely stems from the pre-juvinal molt that nestlings undergo where they grow all 12 tail feathers at the same time instead of two at a time as is typical during the adult pre-basic molt. This rapid growth of all rectrices leaves nestlings and second year birds with characteristically poorer quality feathers (Pyle 1997) that are often ragged by the end of the following year. This pressure for fast simultaneous growth of all tail feathers in nestlings may explain the stronger correlation between color and tail feather growth rate in second year birds. Furthermore, fledglings likely have greater variability in body condition as well as overall poorer body condition compared to

adults. Selection acts strongly on juveniles and there is very low survivorship from fledglings to breeding adults (Bauldry et al. 1995). Condition at time of molt as a juvenile may be crucial in determining the chance of surviving to adulthood.

Males and females showed a significant correlation between feather growth rate and the number of offspring produced, indicating that condition in the autumn of one year can have carry-over effects into the breeding season of the following year. Surprisingly, both males and females also exhibited a significant positive relationship between feather growth rate and the number of offspring produced in the prior year. Chicks are energetically costly to care for and raising a larger number of offspring could leave parents in poorer condition during the following molt. However, adults in better quality territories may be able to raise more offspring and still be in better condition at the end of the season (Individual Optimization Hypothesis (Pettifor et al. 1988)). For this reason, cross-fostering and manipulating brood sizes (e.g. Siefferman and Hill 2005) are needed to disentangle territory quality and individual quality from the cost of raising more offspring.

In this study, even when traits were significantly correlated, the r^2 values are rather low. There may be a strong genetic component to growth rates that doesn't fluctuate with environmental conditions (Gienapp and Merilä 2010), or environmental factors like feather degrading bacteria or ultraviolet light may alter feather coloration in the several months before I was able to catch adults in the breeding season.

The study of condition dependence of structural coloration has few large scale correlative analyses. Further population-wide comparisons of molting condition and

feather coloration are needed before accepting the premise that bright structural coloration is an honest signal of condition in natural populations.

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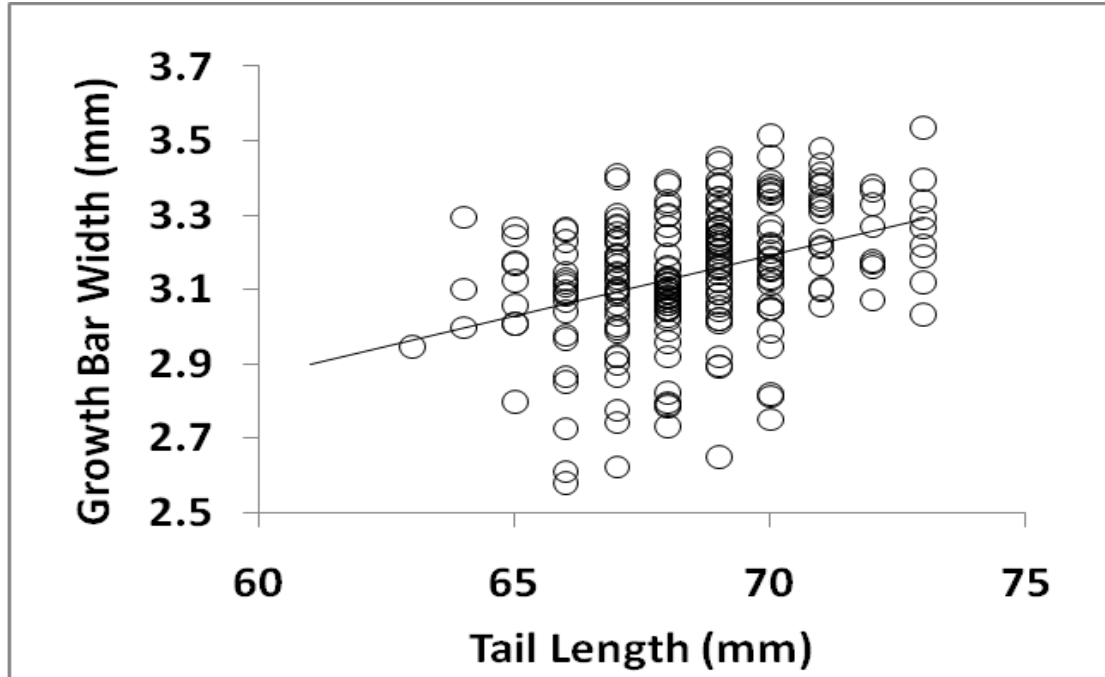


Figure 1. Comparison of tail length and growth bar width in eastern bluebird males.

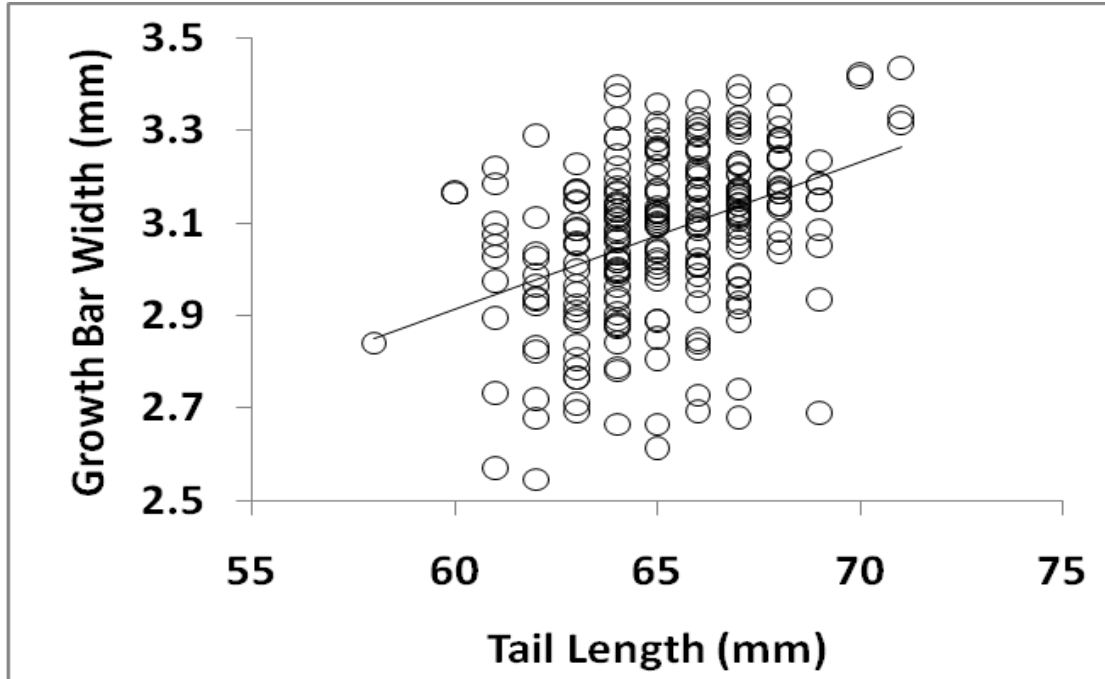


Figure 2. Comparison of tail length and growth bar width in eastern bluebird females.

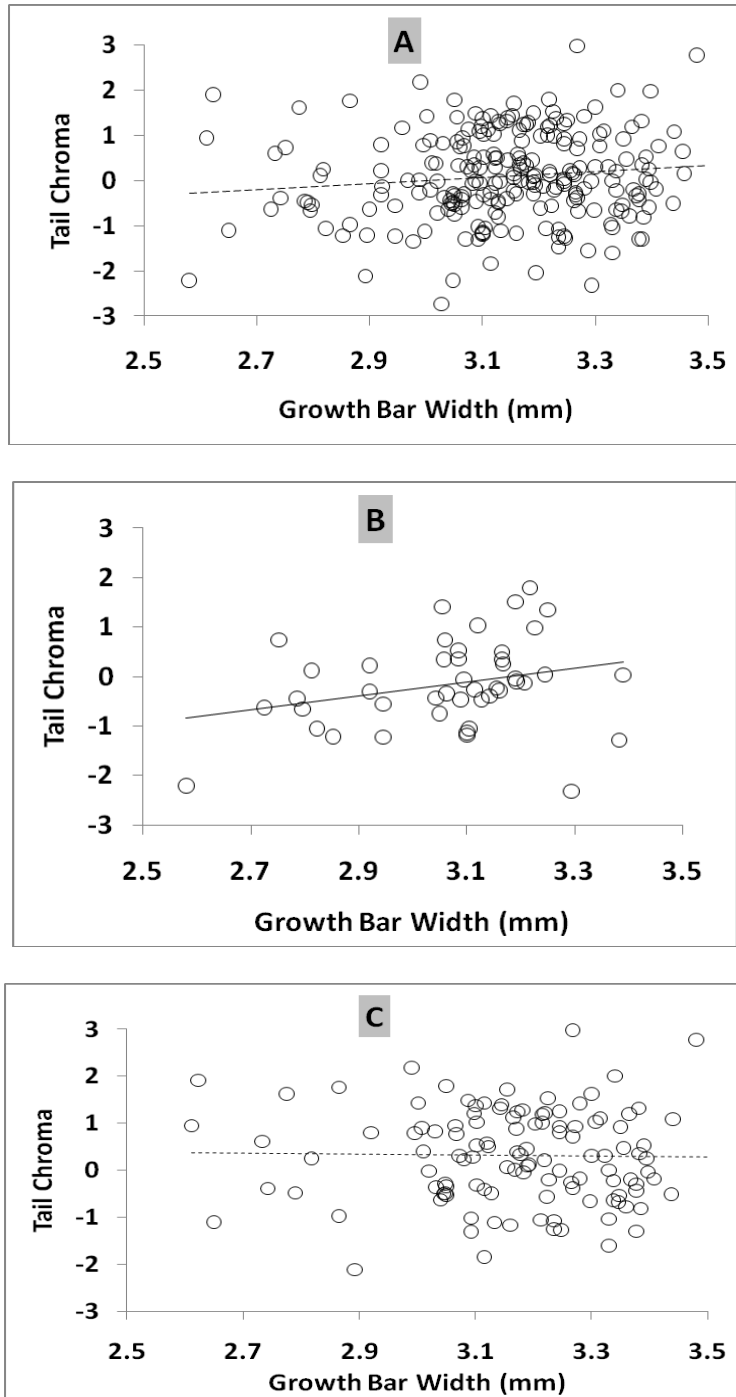


Figure 3. Eastern bluebird tail chroma compared to growth bar width for all males (3A), second year males (3B), and after second year males (3C). Solid lines indicate significant correlation at $\alpha = 0.05$ significance level, dashed lines indicate non-significant correlation.

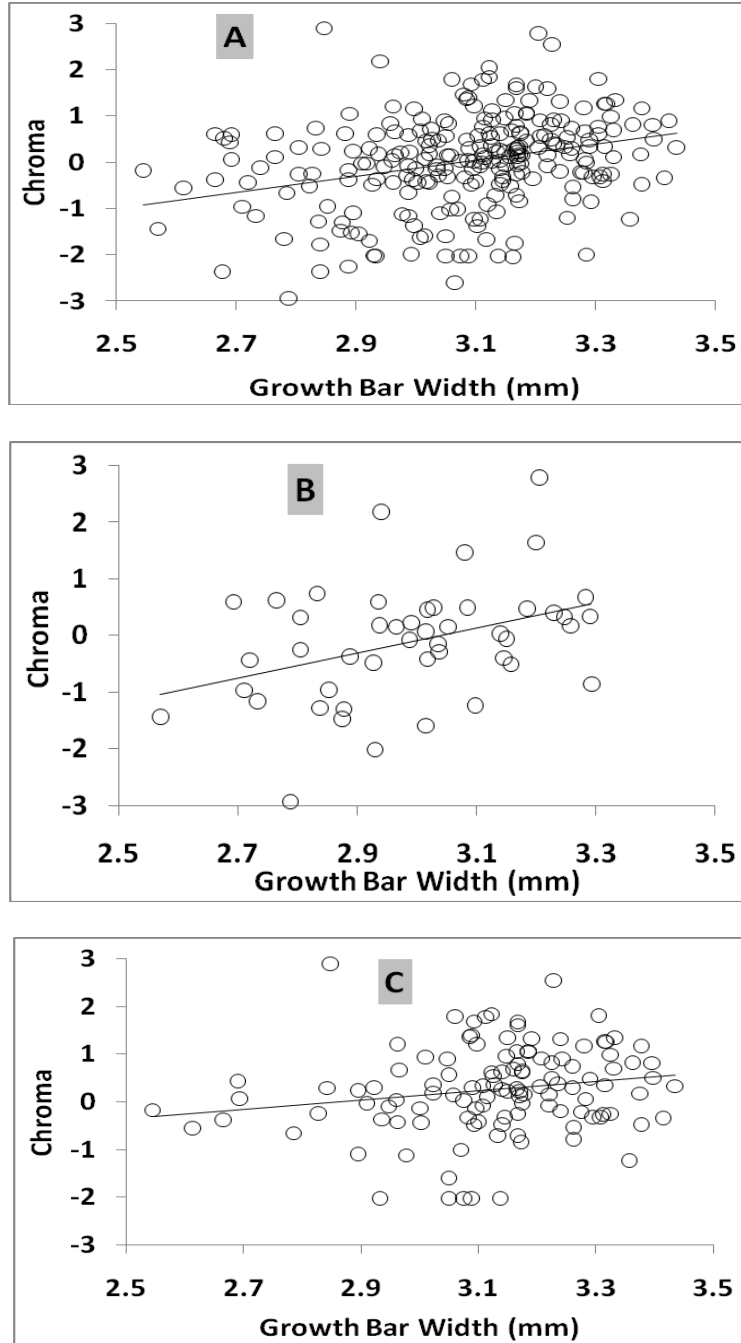


Figure 4. Eastern bluebird tail chroma compared to growth bar width for all females (4A), second year females (4B), and after second year females (4C).

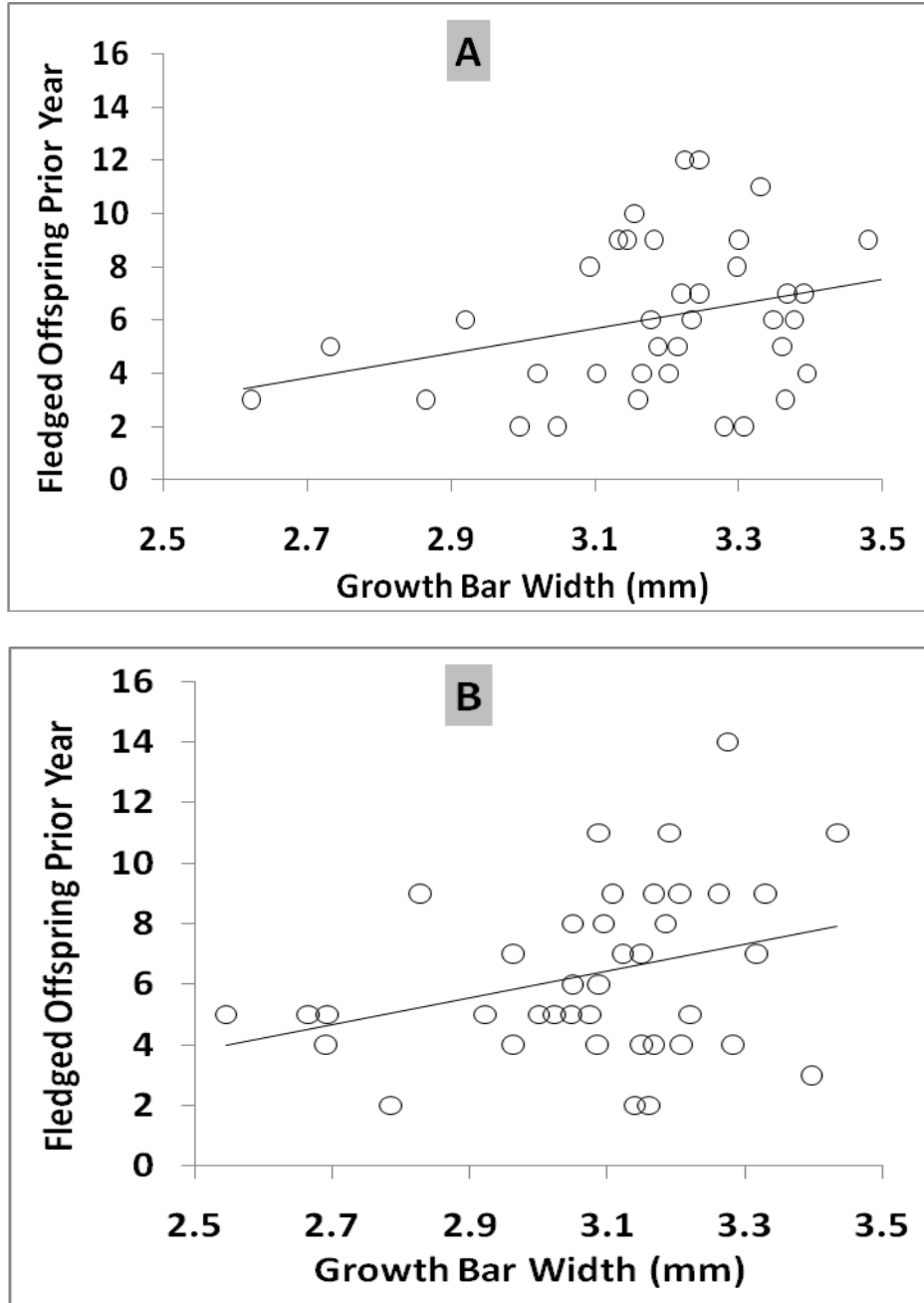


Figure 6. Eastern bluebird feather growth rate compared to the number of offspring fledged in the previous summer for adult males (6A) and females (6B).

CHAPTER TWO

Coloration as a Signal of Status in the Eastern Bluebird

ABSTRACT

Ornamental plumage can function for sexual selection through either attracting mates or threatening rivals. Elaborate ornamentation can be used in male competition as a signal of status if the ornaments are difficult to obtain, even if not useful as weaponry. The eastern bluebird (*Sialia sialis*) is a sexually dichromatic species with males that have bright structurally-based blue plumage as well as melanin-based chestnut plumage. Elaborate male coloration in the eastern bluebird may function as a signal of status during male-male competition for ownership of nestboxes. I tested the signaling function of both ornamental plumage colors by presenting breeding adults with artificially brightened and darkened bluebird models on their territories and recording the attack rate on each model. Bluebird males attacked models with brighter blue coloration significantly more often than models with darker blue coloration. Bluebird males did not attack models with brighter chestnut coloration significantly more often than models with darker chestnut coloration. The structurally-based blue coloration on bluebird wings, back, and tail appears to function as a signal during male competition, whereas the chestnut breast coloration does not appear to influence the amount of aggression from conspecifics.

INTRODUCTION

Sexual selection is the differential ability to secure mates (Darwin 1871) and can occur through either intersexual or intrasexual selection. Intersexual selection (female choice of male traits) potentially leads to elaborately ornamented males while intrasexual selection (male competition) often leads to armaments or weaponry (Andersson and Iwasa 1996). However, male competition can also select for traits that signal fighting ability or dominant status without actually serving as weaponry (Rohwer 1975).

Signaling status can benefit the top males by reducing the number of fights that they must conduct, saving energy and reducing the possibility of injury (Rohwer 1975). Lower-quality males can also obtain some benefit from honestly signaling their low status because high quality males may not expend the effort to fight with low-quality males that are not a direct threat to their territory (Lyon and Montgomerie 1986). For signaling to be honest, lower-quality males cannot cheat and create elaborate ornaments similar to high quality males without the associated costs. Cheating is therefore prevented either by the high cost of constructing or maintaining an ornament (Owens and Hartley 1991) or by the high cost associated with losing competitive battles with high quality males (Rohwer 1977).

Elaborate plumage coloration is the most common type of avian ornamentation, and can come from pigmentation, structural coloration, or a combination of the two. The most common pigments are carotenoids, which provide many of the yellow, orange, and red feather colors (McGraw 2006a), and melanins, which provide brown and black feather colors (McGraw 2006b). Structural coloration is produced from the reflection and

coherent scattering of light at specific wavelengths based on the microstructure of the feathers (Prum 2006) creating various blues, greens, and iridescent colors.

Pigments and feather microstructures have their own synthesis or developmental pathways and may signal different aspects of a bird's lifestyle. Carotenoids cannot be synthesized by vertebrates, so they have to be ingested from food sources (Brockmann and Völker 1934). For that reason, carotenoid-based coloration is thought to reflect the nutritional condition of a bird and its foraging ability (McGraw 2006a). Melanins are synthesized in vertebrates (McGraw 2006b) and do not appear to be limited by nutrition or parasite load (Hill 2006). Thus, melanin-based coloration often reflects the social status of the male and the signal honesty is maintained through frequent testing from rivals (Senar 2006). Coloration and dominance is a topic that has been studied in several species, but most of those species exhibit carotenoid- or melanin-based coloration (reviewed by Senar 2006). Fewer studies have examined male dominance interactions in a species with structural coloration as the status signal.

Eastern bluebirds (*Sialia sialis*) are sexually dichromatic passerines, with males having brighter blue wings and back and a darker chestnut breast than females (Gowaty and Plissner 1998). The chestnut coloration is produced by melanin pigments, but the blue wing and body feathers get their coloration from nanostructures in the wings reflecting light over an ultraviolet-blue range (Shawkey et al. 2003). Sexual dimorphism (in this case dichromatism) can indicate some level of sexual selection with the gender under strongest selection being more elaborately colored (Owens and Hartley 1998). Eastern bluebirds are a secondary cavity nesting species that readily occupy man-made nest boxes. However, in natural settings, the number of available cavities would be a

limiting factor on bluebird breeding, so competition for the few available cavities would be fierce (Newton 1994).

There has been extensive testing of blue coloration as an indicator of male quality in bluebirds, with color being correlated with earlier breeding and greater number of offspring fledged (Siefferman and Hill 2003; Siefferman and Hill 2005). Although the brightness of male blue coloration increases with age, chestnut coloration becomes duller with age (Siefferman et al. 2005). Eastern bluebirds have been shown to be able to discriminate between adult and juvenile chest coloration and divert aggression toward conspecifics with adult chest coloration (Ligon and Hill 2009), however there has been no study on whether the variation in orange chest coloration among adults influences aggression from conspecifics.

Although males grow brighter plumage as they age (Siefferman et al. 2005), and presumably gain experience and competitive ability, experimental tests have shown a lack of female choice for the male with brighter blue plumage when females are presented with two males differing in plumage coloration (Liu et al. 2007). One possible explanation is that bright male coloration serves as a signal of dominance when male birds are making first assessments of a rival's competitive ability. Although this has been proposed for other thrushes (Udvardy 1977), it has not yet been directly tested.

Dominance has been correlated with coloration in other species (summarized by Senar 2006), however it is often unclear whether the brightness of the color itself is the signal or if body condition or other traits are the signal and color is simply correlated with condition. The relative influence of multiple traits is difficult to distinguish in the field and an experimental manipulation of body condition or plumage coloration is required to

separate their relative importance in dominance competitions. Although a previous study assumed brighter males were dominant due to their earlier breeding when nestboxes were limited (Siefferman and Hill 2005), there has not yet been a direct test of color, dominance, and signal detection in eastern bluebirds.

In this study I manipulated coloration on taxidermic models of eastern bluebird males and then presented the models to resident bluebirds during the breeding season. Bluebirds display threatening postures including bill wiping, wing flapping, and singing (Krieg 1969) toward taxidermic mounts in their territory and will violently attack a model bluebird that remains in the territory. By using models, I reduced the problems of interactive behavior between live models and resident pairs that can override any potential signal function of coloration. Furthermore, by artificially manipulating the blue and chestnut coloration of eastern bluebirds, I can test for the importance of each color ornament independent of the age or body condition of the bird.

METHODS

I studied eastern bluebirds at a long-term monitored breeding population in Auburn, Alabama (32°35'N, 82°28'W) from February to August, 2009 - 2010. Male eastern bluebirds defend a territory surrounding a nest box and will attack conspecifics that encroach upon their territory. I conducted behavioral experiments at times when male aggression is high, during egg-laying and chick raising (Gowaty and Wagner 1988), to maximize the behavioral response to intruders. I used taxidermic mounts of eastern bluebirds as models on which I artificially manipulated the brightness of the plumage to test whether the brightness of male bluebird coloration affects aggressive behaviors in

territorial males. I made taxidermic models from male eastern bluebirds that had been collected in prior years. I mounted the models in upright postures and attached each model to a dowel and small PVC fitting. I scanned each model on the breast, head, wing, and rump with an Ocean Optics Optics S2000 spectrometer (Dunedin, Florida) using a 90 degree incident and reflective angle. Each feather patch was scanned three times, lifting the probe off the feathers between scans.

In 2009, I brightened the structurally-based blue coloration on a male bluebird model's head, wings, back, and tail with a violet marker (Prismacolor Violet Mist) and darkened the blue coloration on other models with a black permanent marker (Sharpie Black) (Liu et al. 2007) (Fig.1). These manipulations altered the brightness (total reflectance from 300 to 700 nm) and chroma (proportion of reflectance from 350 to 450 nm) within the range of variation observed in the population without altering hue (wavelength of maximum reflectance). I matched models of similar size, posture, and chest coloration and used six pairs of models to reduce the effect of any one model upon eliciting aggression from territorial males.

In 2010, I increased the chroma and brightness of the melanin-based chestnut coloration on a male bluebird model's breast using a brown marker (Prismacolor Walnut) and decreased the coloration using hydrogen peroxide (White et al. 1980) to bleach the feathers (Fig. 2). I again used six different pairs of models to minimize the influence of a single model on the overall results.

During both years I followed the same protocol: I drove two 1.2 meter rebar poles into the ground five meters away from a bluebird nestbox and five meters apart from each other. Atop each rebar I placed a taxidermic bluebird model attached to a 1.2 meter

wooden dowel (diameter 1cm) placed perpendicular to the rebar. The dowel gave the resident bluebirds a place to perch near the model and display before attacking. One of the models was experimentally darkened and the other model was experimentally brightened. Models were covered with a paper bag and then simultaneously exposed by pulling the bags off the models using thin fishing line attached to the bags. I continuously played a 30 second audio recording of eastern bluebird songs (A Field Guide to Songs: Eastern and Central North America (Peterson Field Guides)) from a speaker placed between the models for five minutes before exposing the models and continued to play the eastern bluebird song throughout the trial to ensure that the resident bluebirds were searching for an intruding adult male before the models were presented and were attentive to the models when they were exposed. Trials ran for 10 minutes after the models were exposed or stopped when the resident bluebirds physically attacked a model to preserve model condition for later trials. Observations were made from a concealed location >30 meters away.

To determine the extent that color influences the first aggressive response from territorial males I quantified which model received the first signs of aggression. I also determined which model received the most aggression and the amount of time until the models were attacked. I analyzed the number of trials that each model was attacked using a Chi-Square goodness-of-fit test.

RESULTS

In 2009, I conducted 66 trials with blue brightened and blue darkened models. Of the 66 trials, seven males did not express quantifiable aggression toward either of the

models. Of the remaining 59 trials, resident males first attacked the blue brightened model significantly more often than the blue darkened model ($X^2 = 4.90$, $N = 59$, $P = 0.03$, Fig. 3). The model that was attacked first was also the model that was attacked most in 48 of the trials (81%). Of the 11 trials where the model receiving the most aggression differed from the model receiving the first aggression, six trials (55%) were a switch from attacking the dark model first to attacking the bright model the most and five trials (45%) were a switch from attacking the bright model first to attacking the dark model the most (Fisher's exact test, $P = 0.99$).

In 2010, resident males did not differ in the number of times that they first attacked the chestnut brightened versus chestnut darkened model ($X^2 = 1.78$ $N = 36$, $P = 0.18$).

DISCUSSION

There are many factors influencing the outcome of competitive interactions. Hormone levels, familiarity with the territory, breeding experience, and current body condition can all influence dominance between two individuals. Since feather coloration is fixed at the time of molt, plumage coloration is not an indicator of the current physiological state of an individual. However, most antagonistic encounters are resolved without an actual fight and signals of status like plumage coloration can allow visual shortcuts to assess the quality of a rival.

Male eastern bluebirds responded to manipulated differences in structurally-based blue feather coloration. Males attacked conspecific models that were artificially brightened significantly more often than they attacked artificially dulled models. These

color differences and behavioral responses match age- and condition-related differences in the brightness of bluebird plumage. Older males and males in better condition are often brighter than younger males and high quality males are likely a greater threat for territory usurpation or cuckoldry. By showing more aggression toward conspecifics that are a greater fitness threat, bluebirds can likely maximize the benefits from aggressively defending a territory.

In contrast to male responses to the structurally-based blue coloration, males did not appear to respond to manipulated differences in melanin-based chestnut breast coloration. Male breast coloration in the eastern bluebird does not become brighter with age; older males actually have less ornamented breast coloration than young males (Siefferman et al. 2005). Since the melanin pigments in the eastern bluebird breast feathers can be synthesized by the individual (McGraw 2006b), variation in bluebird breast coloration may not reflect variation in condition and therefore the breast coloration may not act as a signal of status in this species.

Male competition and female choice are not mutually exclusive selective forces driving elaborate ornamentation, but previous studies of both aviary-based and field-based mate choice experiments have shown a lack of female choice for bright male plumage in the eastern bluebird (Liu et al. 2007). Male competition can be influenced by male coloration, and it is possible that female bluebirds judge males based more on territory quality rather than male coloration. Experimental tests of male competition and female choice can help explain the relative signaling importance of different color ornaments and expand the scope of ongoing studies of sexual selection in the eastern bluebird.

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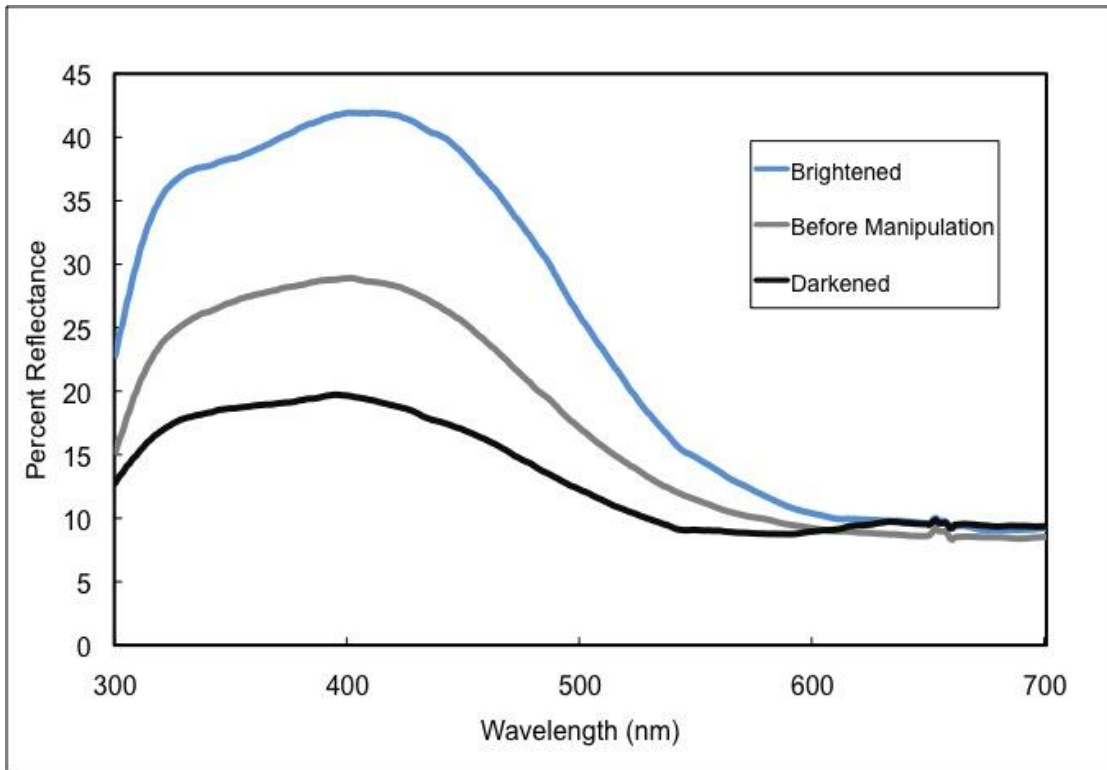


Figure 1. Spectral reflectance of eastern bluebird rump coloration including average reflectance curve (grey line), artificially brightened models (blue line), and artificially darkened models (black line).

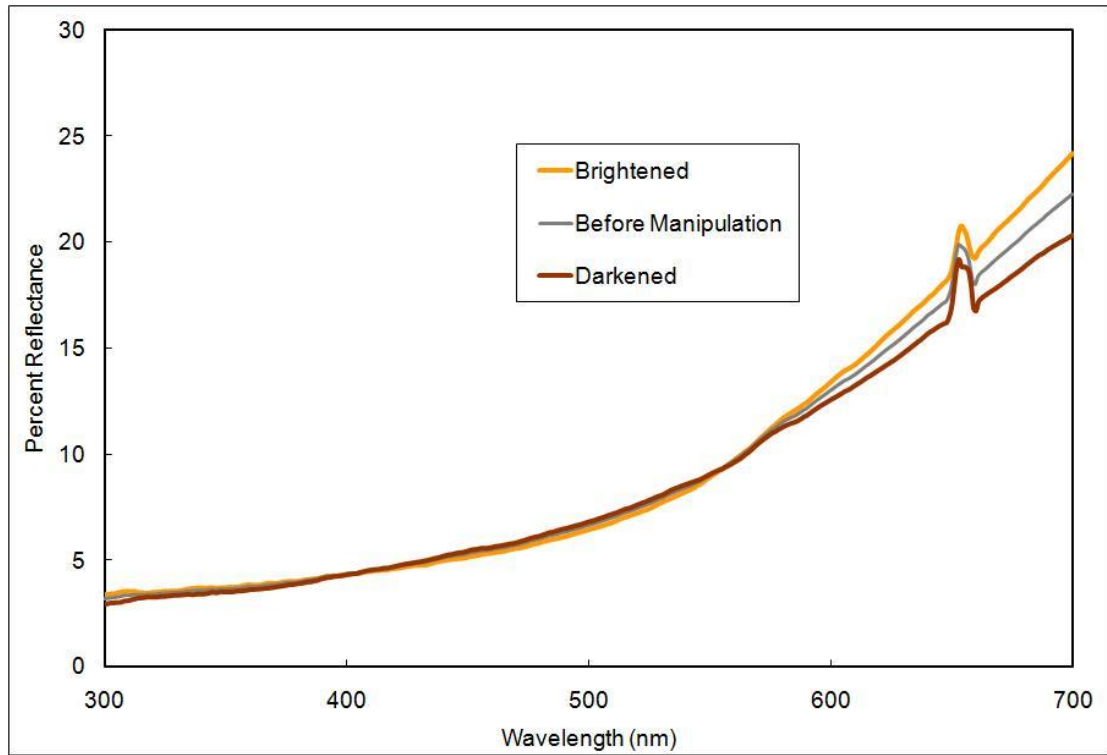


Figure 2. Spectral reflectance of eastern bluebird breast coloration including average reflectance curve (grey line), artificially brightened models (tan line), and artificially darkened models (brown line).

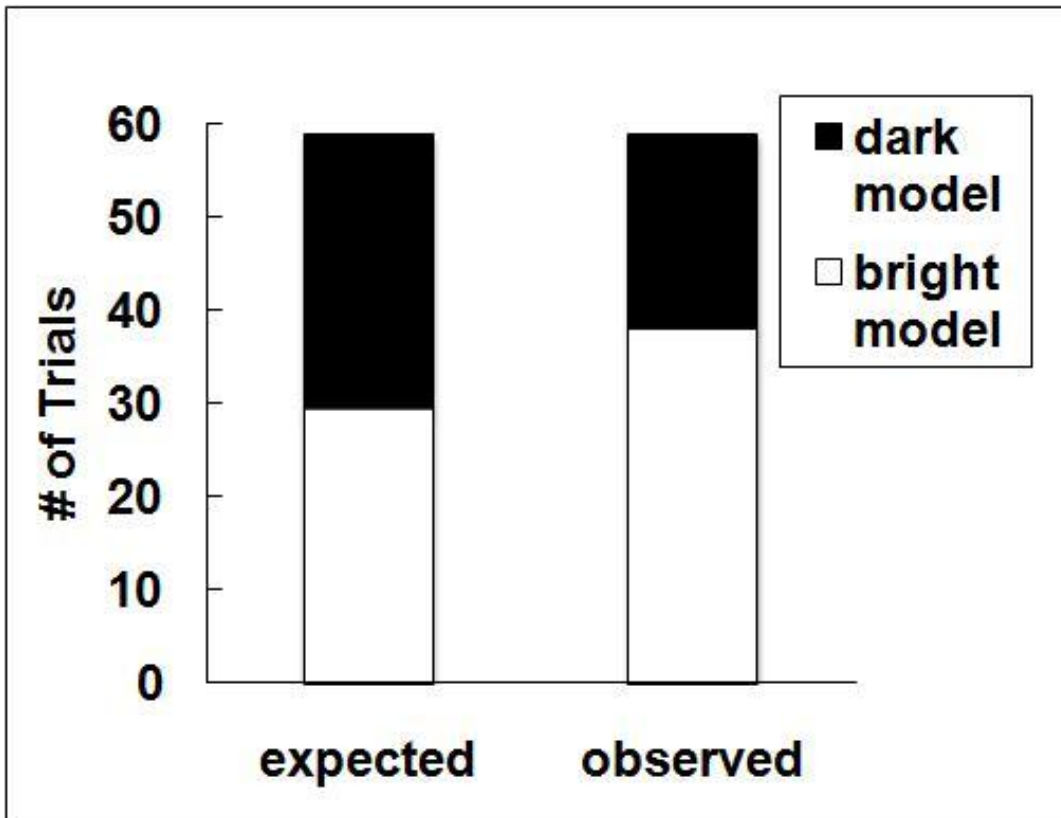


Figure 3. Aggressive responses from eastern bluebirds toward models with experimentally darkened or brightened blue coloration. Bars represent the number of eastern bluebird trials with the first aggressive response toward the experimentally darkened (black bar) or experimentally brightened (white bar).