

Female Plumage Coloration in Eastern Bluebirds, *Sialia sialis*:
Is it a Sexually Selected Trait?

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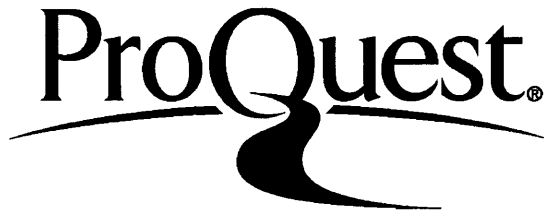
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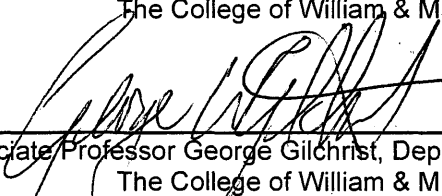
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COMPLIANCE PAGE

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ABSTRACT PAGE

In many animal species, males possess extravagant traits that cannot be explained by natural selection. Instead, sexual selection, which acts on variation in mating and reproductive success, is invoked to explain these apparently maladaptive traits. Males with the most extravagant traits have increased mating and reproductive success because they are either preferred by females or win competitions with other males over access to females. Traditionally, females are considered the choosy sex as a result of a high parental investment in terms of egg production and parental care. However, when males provide parental care the parental investment made by each sex is more balanced. Consequently, some degree of choosiness can benefit both sexes. In the socially monogamous eastern bluebird, *Sialia sialis*, both males and females provide parental care. Additionally, both males and females possess colorful plumage, and within each sex there is among-individual variation in plumage coloration. In this study, I explored whether female coloration is a sexually selected trait that may influence male mate preference. I first compared female coloration to various fitness metrics and found that female tail coloration is weakly predictive of reproductive success, however, rump and chest coloration appear to be unrelated to any fitness metric measured. Additionally, there is evidence of assortative mating by tail coloration suggesting that tail coloration may be an important trait used in male and mutual mate choice. Experimental male mate preference trials revealed that rump and chest coloration do not influence male mate preference; however, preference for tail coloration was not tested. Female rump and chest coloration do not appear to currently be under sexual selection; yet tail coloration may indicate fitness potential and be used in male and mutual mate choice.

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Chapter 1. Female ornamentation: is sexual selection acting on extravagant plumage in females?

Introduction

The occurrence and evolution of extravagant traits in males, such as bright plumage in birds, is often costly; individuals with extravagant traits are more conspicuous to predators and use more energy to produce these traits (Andersson, 1994; Darwin, 1871). However, these costly traits persist and have become more exaggerated over time, despite natural selection acting against them. Darwin described this phenomenon as sexual selection (Darwin, 1871). Males with the most extravagant traits have the highest mating success and, therefore, are more successful at passing on their genes (Andersson, 1994; Andersson and Iwasa, 1996). Classic sexual selection theories are based on the observation that males and females invest different amounts of energy into reproduction and parental care (Trivers, 1972). Females produce expensive eggs, risk predation protecting young, and provide food for young; while males often invest sperm and little else (Trivers, 1972). Consequently, females are limited by the number of eggs they can produce and nurture into viable offspring, while males are limited by the number of eggs they have the opportunity to fertilize. Therefore, females would benefit by being choosy in order to obtain the best possible male investment, be it genes, parental care, or defense against predators, in their fertilized eggs. Males, however, should compete among one another for access to as many females as possible through male-male competition and mate attraction mechanisms (Trivers, 1972). Consequently, a significant portion of sexual selection theory attempts to explain the evolution of female mate preference and exaggerated male traits.

Direct selection on female preferences offers clear and testable predictions about how and why a female chooses a particular male. Sensory bias or sensory exploitation models (Endler and Basolo, 1998; Ryan, 1990) show that males exploit an existing interest in characteristics of a trait (i.e., movement or color) to attract the attention of females. These characteristics are typically reminiscent of cues a female would use for foraging or survival (Ryan, 1990). Consequently, female preference for the male trait is reinforced by natural selection. When females gain direct benefits by mating with particular males, there is also direct selection acting on female preferences (Kokko et al., 2006). These direct benefits can be in the form of nuptial gifts, increased male parental care, or a lower risk of sexually-transmitted diseases (Kokko et al., 2006). There is sexual selection acting on males to produce, or provide, these direct benefits and on females to search for mates that are able to provide them. Unlike sensory exploitation models, natural selection can work against sexual selection for direct benefits (Kokko et al., 2006); once the cost of mate searching and providing benefits are too expensive, natural selection will oppose sexual selection. Chase-away or sexual-conflict mechanisms (Holland and Rice, 1998; Rosenthal and Servedio, 1999) also exert a direct selective pressure on females. Females will evolve defenses to protect themselves from the costs of mating, and in response, males evolve tactics to get around female defenses. Female defenses get stronger, and male tactics overcome them resulting in an evolutionary arms race. While sexual-conflict mechanisms do not necessarily involve a female preference, they are responsible for driving the exaggeration of male traits.

Indirect selection for female preferences is a more controversial explanation for the exaggeration of preferences and their corresponding traits. Evolution by “good genes”

(Fisher, 1915; Lande, 1981; Mead and Arnold, 2004; Zahavi, 1975) states that females choose males based on a trait that might indicate genetic quality, and consequently, offspring will be in better genetic condition. The controversy lies in determining genetic quality. Male traits are often a result of a genotype by environment interaction, and therefore, the potential indirect benefits are difficult to measure. Evolution by runaway selection (Fisher, 1915; Lande, 1981; Mead and Arnold, 2004) is also an indirect process, however, less controversial. Male offspring inherit the preferred trait, female offspring inherit the preference for the trait, and both are exaggerated from generation to generation. However, unlike chase-away, runaway mechanisms represent a coevolutionary process that does not pit the interests of the two sexes against one another, and will continue until opposed by natural selection (Kokko et al., 2006; Mead and Arnold, 2004). Additionally, unlike the “good genes” hypothesis, runaway mechanisms are not dependent on the signaling function of male traits. The two processes are not mutually exclusive, however, traits exaggerated by runaway selection are not always traits that signal “quality” (Kokko et al., 2006; Mead and Arnold, 2004).

A significant proportion of empirical work exploring how and why male traits become so elaborate has focused on female mate choice. However, male-male competition can also be responsible for the exaggeration of male traits, specifically traits and behaviors involved in combat or intimidation (Andersson, 1994). Traits such as horns, spurs, and other weapons are used for battle between males (Andersson, 1994; Andersson and Iwasa, 1996); often the males are competing for a territory or access to females. Additionally, bright coloration and other conspicuous signals can be badges of status that signal a male’s competitive ability (Andersson, 1994; Andersson and Iwasa,

1996). Consequently, conspicuous traits not used for battle can also be targets of selection via within-sex competition mechanisms.

Much of the theoretical development for sexual selection and the empirical emphasis of field and laboratory experiments have focused on the evolution of ornaments in males (Andersson, 1994; Andersson and Iwasa, 1996; Smith, 1991). Darwin himself viewed the evolution of extravagant traits in females as a result of correlated selection on male traits that were also expressed in females (Darwin, 1871). Therefore, until the early 1990s, cases of female ornamentation were often ignored or assumed to be a result of a correlated response to selection for male traits (Lande, 1980, 1987). However, in socially monogamous species, where males provide a significant amount of parental care, the investment made by males and females is more balanced. Consequently, we should expect a gradient of choice and competition in both sexes (Burley, 1977; Johnstone et al., 1996; Kokko and Johnstone, 2002). Male mate choice and female-female competition should no longer be considered oddities of species with reversed sex roles, but rather a reflection of parental investment and the limitations of either sex. In this review, I will concentrate on presenting the evidence of sexual selection acting directly on female ornamentation. In the literature there is a bias toward female ornamentation in birds, consequently, much of my focus will be on sexual selection acting on ornamental plumage.

Male and Mutual Mate Choice in Birds

Mate preference should not be limited to one sex; instead, the degree of choosiness should represent the parental investment of each sex (Burley, 1977). In socially

monogamous birds, both males and females provide a significant amount of parental care and should therefore both express some degree of mate choice. Burley (1977) first experimentally tested this idea using feral pigeons (*Columba livia*) and demonstrated that males do express some degree of selectivity. However, there are distinct color and pattern morphs in feral pigeon plumage. Focal males were given a choice between different plumage polymorphisms and experiments were geared towards testing a male's preference in relation to his own phenotype. In the early 1990s the first studies demonstrating male mate preference for continuous female traits provided convincing evidence of male mate choice in socially monogamous birds (Hill, 1993; Jones and Hunter, 1993). By manipulating crest length of male and female crested auklet (*Aethia cristatella*) mounts Jones and Hunter (1993) found that mounts with the longest crests received the most displays from the opposite sex. Hill (1993) also experimentally tested whether males showed a preference for more colorful females in house finches (*Carpodacus mexicanus*). When presented with four females with varying degrees of red plumage, males preferred females with plumage manipulated to be the most colorful.

Experimental studies that directly test for male preference, such as the previous examples, provide straightforward evidence for or against male mate preference. Additionally, by manipulating plumage traits, confounding factors, such as body size and female behavior, can be controlled and the response seen in males can be attributed to the variation in the plumage trait rather than another variable. Unfortunately, many studies that explore male and mutual mate choice do so indirectly by looking for assortative mating and using the onset of breeding as a proxy for choice (e.g., Griggio et al., 2005; Hill, 1993; Jawor et al., 2003; MacDougall and Montgomerie, 2003; Safran and McGraw,

2004). While these studies can provide insight into whether male mate choice is occurring, they are far from conclusive. Factors other than sexual selection can contribute to assortative mating and early breeding. One example is when there are resident and migrant populations in one area. If the two populations differ slightly in coloration, and interbreeding is rare, there will be evidence of assortative mating by color, but not necessarily as the result of mate choice. Additionally, coloration and onset of breeding may both increase with some other variable such as age, producing a spurious relationship between color and onset of breeding. Studies that demonstrate assortative mating and early breeding can be used as a starting point; however, direct examination of what dictates those patterns is needed to determine whether they reflect male and mutual mate choice.

While choosiness is largely determined by parental investment (Burley, 1977; Johnstone et al., 1996; Kokko and Johnstone, 2002), there must also be some benefit to making a choice. For males, this benefit is typically female fecundity and reproductive success. For example, in zebra finches (*Taeniopygia guttata*) males provide a significant amount of parental care and demonstrate a preference for more fecund females (Jones et al., 2001; Monaghan et al., 1996). However, if there were little variation in female fecundity and reproductive success, males would gain little from being choosy. Consequently, male preference should reflect a choice for fecund and successful females. Typically, females are the higher-investing sex, even in species with biparental care, and there is likely more variation in parental quality of the higher-investing sex (Parker, 1983). Consequently, one can argue that males may actually gain more through mate choice than females (Deutsch and Reynolds, 1995; Parker, 1983). However, this

argument does not account for sex differences in the cost of mate choice, which are a result of rejecting a potential mate and the time needed to find a new mate. This in turn is dictated by the operational sex ratio resulting from the proportion of each sex in the breeding population and the amount of parental care provided by each sex (Johnstone et al., 1996). In populations with approximately equal numbers of males and females, parental investment appears to be the most important determinant of choosiness. In biparental species where care is shared equally the benefits of choice can be high for both sexes and other variables such as adult sex ratio, population density, and the rate at which individuals interact will determine cost of choice and the choosiness of either sex (Johnstone et al., 1996; Kokko and Johnstone, 2002).

While female preferences are thought to evolve as a response to both direct and indirect benefits, it is unlikely that indirect benefits contribute to the evolution of male preferences. Male preferences are more sensitive to costs accrued by rejecting potential mates. Even in biparental species where parental care is shared somewhat equally, females have a higher parental investment in terms of egg production. Consequently, males must gain direct benefits in terms of higher fitness to offset these costs. For example, in dark-eyed juncos (*Junco hyemalis*), a socially monogamous biparental species, males show no preference for females with experimentally increased tail white (Wolf et al., 2004). However, there is no evidence that increased tail white indicates that a female has a fitness advantage. While tail white increases with age (Wolf et al., 2004), age is not necessarily indicative of success or parental quality. Therefore, male and mutual mate choice should only be seen when certain criteria are met: (1) there must be a low cost to choice relative to the benefit gained by being choosy; (2) there must be

variation in female fecundity and reproductive success; and (3) the preferred female traits must reflect variation in female fecundity and reproductive success.

Female Ornamentation as a Signal

Male preference is unlikely to be the mechanism driving female ornamentation unless the preferred female traits indicate something about the fecundity or potential reproductive success of the female. In other words, the males need to gain some direct benefit from being choosy. Hence, studies of male mate preference should also assess the signaling function of the female trait. Skeletal size, body mass, and body condition (typically defined as mass corrected for skeletal size) are often considered metrics of individual quality and are potential indicators of fecundity. In female ectoderms, body size, particularly abdomen size in insects, is often representative of fecundity (Bonduriansky, 2001). While this relationship is less common in endoderms, it has been shown in some bird species that body mass and condition relate to fecundity (e.g., Barbraud, 2000; Sæther et al., 1997). Therefore, males could use ornamentation related to body size, mass, or condition when making mate choice decisions to increase their overall fitness. For example, in rock sparrows (*Petronia petronia*) males and females possess a yellow breast patch; in females, the size of the breast patch is positively correlated with body mass (Pilastro et al., 2003). Males used this information and courted females with experimentally reduced breast patches less often (Griggio et al., 2005) and reduce their nest attendance and sexual activity when their mate's breast patch was reduced after egg-laying (Pilastro et al., 2003).

Immunocompetence and parasite resistance are also measures of individual quality and can be reflected in plumage ornamentation. Hamilton and Zuk (1982) proposed a link between immunocompetence and coloration, a relationship that has been examined extensively with regards to carotenoid-based plumage coloration (e.g., Brawner et al., 2000; Lozano, 1994). Carotenoids are a dietary pigment responsible for the production of most red, orange, and yellow plumage colors; however, they also play important roles in physiological process such as free-radical absorption, support of steroid synthesis and cancer prevention (Olson and Owens, 1998). Therefore, a birds' health, measured as immunocompetence or parasite resistance, can be assessed by the coloration of its plumage; the healthiest birds can afford to sequester enough carotenoids to create rich colors and the least healthy birds must use most of their dietary carotenoids as antioxidants rather than pigment (Blount, 2004; Houde and Torio, 1992; Møller et al., 2000; Olson and Owens, 1998).

Males that choose to mate with females that express carotenoid-rich plumage are potentially lowering their own risk of infection and increasing the probability that their mate will survive and provide parental care to offspring. In great tits (*Parus major*), the hue of carotenoid-based yellow plumage correlates to infection by blood parasites. Males and females with more blood parasites had significantly lower hue values for yellow plumage (Horak et al., 2001). Additionally, individuals that survived had higher hue values than non-survivors (Horak et al., 2001) indicating that the condition-dependent yellow plumage may signal individual quality in terms of survival probability.

Carotenoids are also an important pigment for egg yolk production; developing embryos have a high rate of oxidative metabolism, and carotenoids protect cells from damage by

free radicals (Blount et al., 2000). Consequently, carotenoid-based signals may have a unique function in females. Females that express rich carotenoid-based colors may be advertising their ability to lay carotenoid-rich eggs (Blount et al., 2000; Blount et al., 2002) and in turn, produce healthier offspring (Blount et al., 2000; Blount et al., 2002).

Sexual selection operates on variation in mating and reproductive success; therefore traits that correlate with mating and/or reproductive parameters could be targets of sexual selection. In addition to quality egg production, mating and reproductive success can be measured as onset of breeding and fitness parameters such as offspring condition and number of offspring produced. In female eastern bluebirds the brightness and purity of blue coloration of rumps and tails relate to the onset of breeding, offspring condition, and maternal provisioning rate (Siefferman and Hill, 2005b). In northern cardinals (*Cardinalis cardinalis*) female underwing color is predictive of female feeding effort (Jawor et al., 2004; Linville et al., 1998). In another example, yellow collar coloration of female blue tits (*Cyanistes caeruleus*) is positively related to clutch size and fledgling success (Doutrelant et al., 2008). However, there is no evidence that males use these traits in mate choice, and as a result, the function of these colorful ornaments is still unclear.

While the preceding examples show that female ornamentation can indicate aspects of individual quality and reproductive success, and in a limited number of cases, are preferred by males, in my assessment there is insufficient evidence to definitively state that female ornamentation is currently a sexually selected trait in most bird species. The link between ornamentation and quality could equally be explained by genetic correlations (Amundsen and Pärn, 2006; Bonduriansky and Rowe, 2005); for example, if

males in better condition produce brighter plumage, it is likely that females in better condition also produce brighter plumage because they share the genomic structure that links trait expression with individual quality that has evolved in males. Additionally, in species such as bluethroats (*Luscinia s. svecica*), where males show a preference for female ornamentation, however the function of that ornamentation is unknown (Amundsen et al., 1997; Smiseth and Amundsen, 2000), male preference could also be a correlated response to selection on female preferences (Mead and Arnold, 2004; Servedio and Lande, 2006). In my view, researchers must provide direct evidence of a functional mating selective pressure acting directly on female ornamentation before labeling it as a sexually selected trait.

Female-Female Competition in Birds

Within-sex competition is also a mechanism of sexual selection that can drive the elaboration of conspicuous traits (Andersson, 1994; West-Eberhard, 1983a). Females may be limited by access to mates, adequate nesting sites, or other reproductive resources, and consequently, compete with each other for them. Aggressiveness and competition are well documented in females of species where nesting sites are limited; for example, species that use secondary cavities are often extremely limited by suitable nesting sites (Gowaty and Plissner, 1998; Rosvall, 2008). In tree swallows (*Tachycineta bicolor*) more aggressive females have a higher probability of acquiring a nest box when cavities are artificially limited (Rosvall, 2008), indicating that female competition is an important process involved in determining which females will have the opportunity to breed. However, of the 113 species of birds with spurs, in only 16 are females armed with

spurs, and there are no species where only females possess spurs (Andersson, 1994). This may suggest that competition mechanisms are unlikely to select for female weaponry. Alternatively, female-female competition should select for conspicuous traits that can be used as badges of status. Females face a higher energetic cost (e.g., egg production) than males during the breeding season and consequently should avoid potentially violent encounters. Therefore, conspicuous plumage may be used for intra-sexual communication and allow females to assess their competitors without physical combat.

If conspicuous female plumage is in fact used in intra-sexual communication and competition, we should expect to see relationships between conspicuous plumage and levels of aggression and dominance. In least auklets (*Aethia pusilla*), whiter plumage is associated with higher social status and individuals with whiter plumage are more likely to win in agonistic interactions (Jones, 1990). Additionally, models with whiter plumage are approached less often compared to models with darker or intermediate plumage (Jones, 1990). In this species, plumage coloration signals social status, allowing birds to avoid aggressive interactions. While this study did not differentiate between males and females, a study in a related species, crested auklets, also showed that males and females with longer crests are more likely to win in agonistic encounters against same-sex individuals with smaller crests (Jones and Hunter, 1999). However, males and females respond differently when presented with same sex models of varying crest length (Jones and Hunter, 1999). Males were less likely to attack models with long crests, but females showed no difference in attack behavior. Similarly, plumage coloration of female red-wing blackbird (*Agelaius phoeniceus*) models did affect whether females showed an aggressive response to the model (Muma and Weatherhead, 1989). These examples do

not support the hypothesis that female plumage allows females to avoid aggressive encounters.

While the previous hypothesis, that more ornamented females actually avoid physical encounters, is an attractive explanation for female ornamentation, there have been very few experimental tests of whether this occurs. Rather, female ornamentation is more often compared to levels of aggression or social status. For example, the size and color of the black face mask in female northern cardinals predicts the level of aggression directed towards a model simulating an intruding female (Jawor et al., 2004). In European starlings (*Sturnus vulgaris*) spottiness and whiteness of chest plumage are positively correlated to dominance and experimental manipulations of spottiness revealed that spottier birds were dominant over less-spotty birds (Swaddle and Witter, 1995). There is some indication in birds that males prefer dominant females and social hierarchies are important in determining who mates with whom (Bolund et al., 2007; Johnson, 1988). Consequently, plumage that indicates dominance may also be important in mate choice.

Female competition strictly for males is another phenomenon that lacks solid empirical support; however, the existing evidence indicates that females of some species compete with one another for mates. For example, in white-throated sparrows (*Zonotrichia albicollis*) white-striped morph females outcompete tan-striped morphs for the more desirable tan-striped males (Houtman and Falls, 1994). Additionally, in blue tits, “divorce” during the breeding season is potentially driven by female-female competition where a new female outcompetes the breeding female for either the territory or the male

(Valcu and Kempenaers, 2008). These examples suggest that female-female competition for males will likely occur when males, or desirable males, are limiting.

Female Plumage Ornamentation as a Sexually Selected Signal

In birds, there is evidence of male mate choice (e.g., Amundsen et al., 1997; Hill, 1993; Jones and Hunter, 1993; Monaghan et al., 1996), of female ornaments acting as an indicator of quality (e.g., Doutrelant et al., 2008; Jawor et al., 2004; Safran and McGraw, 2004; Siefferman and Hill, 2005b), and of female-female competition (e.g., Houtman and Falls, 1994; Jawor et al., 2004; Jones and Hunter, 1999; Swaddle and Witter, 1995).

However, there are very few studies in which the driving force behind maintaining the relationship between female ornamentation and some measure of quality or success has been identified as either male mate choice or female-female competition (see Griggio et al., 2005; Pilastro et al., 2003). All of these phenomena (i.e., male mate choice, female ornamentation, and female-female competition) could be correlated responses by one sex to selection for the trait in the other sex (Lande, 1981, 1987; Mead and Arnold, 2004).

Therefore it seems relevant to ask how likely is sexual selection to act directly on female traits?

Price and Birch (1996) examined the evolution of color dimorphism in passerines and found that female change is just as likely to be the stimulus driving the evolution of dichromatism (or monochromatism) as male change. Similarly, direct selection on female size, either natural or sexual, can result in sexual size dimorphism as often as direct selection acting on male size (Karubian and Swaddle, 2001). This suggests that change in female ornamentation, and its relationships to reproductive and fitness metrics, is not

always a result of a genetic correlation. Selection, for example male mate choice or female-female competition, acting directly on females, can uncouple the correlation between male and female traits. Additionally, selection can act more strongly on female traits than male traits (Karubian and Swaddle, 2001; Price and Birch, 1996) and drive the evolution of ornaments that are not merely a result of a correlated response to selection on males. It appears that sexual selection on females is just as likely to change female traits as sexual selection on males is to change male traits.

If selection acting on female traits should be relatively common, why are there not more definitive examples? One answer is that sexual selection on female traits has not received as much empirical attention as male traits, and as a result, little is known about direct selection acting on female traits. However, the complete answer is likely more complicated. Game theory and population genetic models offer specific predictions about when male mate preference can persist and drive the evolution of female ornamentation. Kokko and Johnstone (2002), using a game-theoretic model of choosiness, signaling, and parental care show that mutual mate choice is unlikely to evolve unless biparental care is essential to offspring survival. Consequently, in species where one sex can compensate for the absence of the other, mutual mate choice and ornamentation may not evolve. Instead, the higher investing sex should become choosy and the lower investing sex should become competitive (Kokko and Johnstone, 2002). Ihara and Aoki (1999) constructed a population genetic model of male mate choice in monogamous mating systems. In their model, male mate choice was dependent on resources. Resource-rich males were able to act on their preference and attract the desired females, but resource-poor males were not able to attract desirable females and consequently could not act on

their preference (Ihara and Aoki, 1999). Therefore, male resources are an important factor in determining choosiness. The predictions of both models need to be empirically tested to determine whether parental investment has been overemphasized as a determinant of choice and its affect on female ornamentation.

In order for a trait to evolve, it must be heritable; however, the heritability of female traits remains a virtually untouched area of research. Heritability of female traits will likely be difficult to disentangle from maternal and environmental effects; however, it is necessary information to determine the potential for an evolutionary response to selection on female traits. Female-female competition is also understudied; more experimental studies of how ornamentation affects physical encounters, aggressiveness, and dominance are needed. Correlational studies of female ornamentation and aggressiveness provide limited insight into causation. Are females more aggressive because they have conspicuous plumage, or are females with conspicuous plumage in turn more aggressive?

Comprehensive research programs are necessary if we wish to truly understand the function of female ornamentation. Studies should encompass both the signaling function of the female ornament and the mechanism driving the variation in that ornament. Additionally, manipulative experimental studies will provide insight into how variation in the trait affects fitness parameters and selective pressures. Correlational and observational studies should be a starting point, not a conclusion. Other variables, such as those in models of male and mutual mate choice, should also be documented. What is the cost of choosiness? Is biparental care necessary to offspring survival? What resources do the males hold? Is there variation in the degree of choosiness that depends on a male's

resources? Large research programs that address these questions will begin to reveal the true frequency of male and mutual mate choice, and female-female competition, and provide empirical support to predictions of when to expect each mechanism.

Beyond Plumage

This review has concentrated on sexual selection acting on female plumage in socially monogamous birds with traditional sex roles. However, this is likely a limited sample of the occurrence of female traits that may be sexually selected. While there is a significant bias towards birds and ornamental plumage in the literature, there are a number of studies that have explored the function of female ornamentation in other taxa such as fish, lizards, and mammals.

In monogamous, biparental species, the parental investment is somewhat balanced between the sexes and some degree of choosiness can benefit both sexes. However, in other mating systems, such as polygyny or polygynandry, the expectations about male choosiness change. In these systems, the cost of rejecting a potential mate increases for males, consequently, males should be less choosy (Johnstone et al., 1996). However, in some lizard species with polygynous or polygynandrous mating systems, males show some degree of choosiness (LeBas and Marshall, 2000; Watkins, 1997; Weiss, 2002). Interestingly, in these species the female ornamental trait is coloration that fluctuates with reproductive status. Clearly, there is a large benefit to males for choosing receptive females. However, female coloration is more likely a byproduct of hormone changes rather than the result of a direct selective pressure, and males are able to exploit this to increase their fitness. Similarly, in polygynous fishes, males show a preference for

females displaying colorful bellies that typically reflect the carotenoid-pigment of the eggs carried by the female (Amundsen and Forsgren, 2001; Kraak and Bakker, 1998; Nordeide, 2002; Pizzolon et al., 2008). In most of these species males tend to the eggs and therefore have a high parental investment. Given that the coloration of females' bellies is likely a reflection of fecundity, and males have a high parental investment, it is not surprising that males prefer the females with the brightest bellies (Amundsen and Forsgren, 2001; Nordeide, 2002; Pizzolon et al., 2008).

Male mate preference and female ornamentation follow the same pattern in mammals, specifically primates. Female coloration fluctuates with reproductive status and receptivity, and males in turn prefer or court more intensely the receptive females (Setchell et al., 2006; Waite et al., 2006). In all these examples, the benefit to males is clear: by choosing receptive females, males are more likely to be successful at inseminating a female. These examples, while they clearly demonstrate male preferences, can be explained by natural selection rather than sexual selection. It is maladaptive for males to court and attempt to mate with females that are not ready or able to reproduce. Consequently, there is a need for studies in taxa other than birds that explore the function of female traits that do not fluctuate with reproductive status, but rather vary in level of expression among females.

Alternatives to Sexual Selection

In this review, I have presented the evidence for female ornamentation as a sexually selected trait. However, a number of other hypotheses have been proposed to explain the evolution of female ornamentation. The genetic correlation hypothesis, as previously

mentioned, states that females are colorful because they carry the same genes as males and there is selection acting on male coloration (Lande, 1980, 1987). This hypothesis is typically invoked when males and females have similar color traits (Muma and Weatherhead, 1989). In such cases, natural selection for cryptic coloration in females is often used to explain why females are typically drab compared to their male counterparts (Amundsen, 2000b; Dunn et al., 2001; Martin and Badyaev, 1996). Second, coloration can be a reflection of sex hormone levels in females, especially in species where not all females are colorful (e.g., house finches) (Kimball, 2006). As with the genetic correlation hypothesis, coloration as a reflection of sex hormones is a by-product of another physiological process (circulating hormone levels), and does not represent selection acting on female coloration. However, unlike the examples in lizards, fishes, and mammals, plumage traits do not change until the next molt (outside of abrasion and wear); consequently, males cannot use these traits as an indicator of reproductive status. Female coloration may also have evolved by natural selection processes, such as species recognition or concealment of sexual identity to avoid harassment (see Amundsen and Pärn, 2006).

Research Needs

While there is compelling evidence to indicate that female ornamentation may be a result of direct selection on females, much of this evidence comes from larger studies of male ornamentation (e.g., Safran and McGraw, 2004). As a result, experimental studies of the function of female ornamentation are lacking. To address this, more research programs focusing on female ornamentation, rather than male ornamentation, are needed. There are

also several studies that have addressed female ornamentation directly (e.g., Amundsen et al., 1997; Siefferman and Hill, 2005b; Swaddle and Witter, 1995), however, these tend to focus on only one piece of the puzzle at a time. Female ornamentation has been assessed in terms of reproductive success, or mate preference, or competition, but rarely all three. In reality, when males and females are both investing in the offspring, and there is variation in quality of both sexes, both males and females should exhibit some degree of choosiness and competitiveness. Consequently, by only addressing one or the other, information is lost. Additionally, theory predicts that there are external factors, other than parental investment and variation in quality, which may affect choice and competition. Hence, a closer examination of the mating systems and costs of choice will provide better insight into which species are more or less likely to exhibit male mate preference and/or female competition.

Heritability is another important piece of the puzzle that is currently missing. Without some degree of heritability, evolution cannot act on traits; therefore, demonstrating the heritability of female traits should be a top priority. In terms of plumage, knowledge of the genetic basis of even coloration is limited, even in males (Mundy, 2006). Obtaining a reliable estimate of heritability will be challenging, particularly in birds. Plumage coloration of offspring cannot be measured until the following breeding season due to molt patterns, making sample sizes dependent on return rates and offspring survival, which are often low. Despite this, I recommend cross-fostering experiments to tease apart effects of genetics and environment. If done on a large scale, over a period of time, a decent measure of heritability could be obtained.

While studies of heritability will be huge undertakings, they will provide valuable insight into the evolution of female ornamentation.

Colorful ornaments are considered costly to produce and there is no question that that different colors are produced by different mechanisms (McGraw, 2006a; see McGraw, 2006b; Prum, 2006). Melanin-based plumage (blacks, browns, grays, rufous and buff colors) is thought to be relatively cheap to produce compared to carotenoid- and structurally-based plumage. In this respect, it is noteworthy that there is some evidence that body condition may be more often linked to the more costly colors (i.e., carotenoid-based reds and yellows and structurally-based blues and iridescent colors) (McGraw and Hill, 2000; McGraw et al., 2002; Siefferman and Hill, 2005b). For example, in female eastern bluebirds (*Sialia sialis*), an experimental study of nutritional stress revealed that the coloration of structurally-based blue rump plumage, but not the melanin-based chestnut breast plumage, was condition-dependent. Females that experienced nutritional stress before and during molt produced significantly duller structural blue plumage than control females, however, there was no difference in melanin-based breast coloration between the two groups (Siefferman and Hill, 2005b). Despite these results, and those of similar studies, a meta-analysis comparing melanin- and carotenoid-based sexual signals found no difference between the two in terms of condition dependence (Griffith et al., 2006).

While it appears that different pigment types are do not generally differ in their effectiveness at signaling condition (Griffith et al., 2006), the possibility that different colors are used for different types of signals remains. Dietary pigments may be more indicative of an individual's foraging capacity and therefore of their potential parental

quality. Consequently, they may be used as a signal in mate preference. In females, carotenoid-based plumage may signal that a female can produce quality eggs (Blount et al., 2000; Blount et al., 2002) and therefore be used for male mate choice. Additionally, since the realization that most birds are sensitive to UV light (e.g., Bennett et al., 1994), it has been proposed that UV signals serve as a private communication channel for birds (Banks, 2001; Hunt et al., 2001). This theory is strengthened by the fact that more so than any other color, UV signals are strongly associated with areas used in courtship displays (Hausmann et al., 2003). Consequently, it appears that particular colors (i.e., UV-reflecting and dietary pigments) may be more likely to be sexual signals than other colors. More comparative studies are needed to test the likelihood of this hypothesis.

Another important step towards truly understanding the occurrence of ornamental traits in females is to broaden the scope of empirical evidence. Currently, there is a bias towards studies of female ornamentation in passerine birds. While there is evidence of male mate choice and female ornamentation in other taxa (i.e., lizards, fishes, mammals), the female traits so far examined are fundamentally different from the examples in birds, and likely represent responses to natural selection rather than sexual selection (e.g., Amundsen and Forsgren, 2001; Setchell et al., 2006; Weiss, 2002). Additionally, the abundance of studies in birds results in a high proportion of research exploring ornamental plumage. However, female ornamentation is not limited to plumage; females can use skin, eyes, and even vocal behavior as sexual signals. Consequently, future work should include studies of traits potentially under sexual selection in females of taxa other than birds and tissues other than plumage.

More so than males, females face an energetic trade-off between producing extravagant traits and reproduction. Consequently, there may be a moderate level of ornamentation that maximizes a females' ability to signal and successfully reproduce. This could be particularly true for carotenoid-based traits where females must trade-off between sequestering carotenoids for ornamentation or egg production (Blount et al., 2000). Studies that look for stabilizing selection on female ornamentation are rare, however Chenoweth and colleagues (2006) show that in theory, when there is a trade-off between ornamentation and reproduction for females, male preference can exert a stabilizing selective pressure. Directional selection is not the only type of selection that can act on female traits, and other types should also be explored in the future.

Conclusions

There is no question that, in some bird species, females possess conspicuous and ornamental plumage. The question is why do females possess ornamental plumage. While the perception of female ornamentation has gone from it being a correlated response to it being a result of sexual selection, there is not enough empirical evidence to support any hypothesis for why females are ornamented. More attention must be paid to female traits. The selective pressures acting on both sexes drive the evolution of the species, therefore, concentrating on males, as has been the case historically, only tells half the story. Understanding the function of female ornamentation, and the selective pressures acting on it, will provide a better understanding of the species as a whole.

Chapter 2. Exploring the function of female coloration in eastern bluebirds *Sialia sialis*

Introduction

It is generally accepted that males express extravagant ornaments as an evolutionary response to sexual selection driven by female preference and/or male-male competition (Andersson, 1994). However, there is no similarly accepted explanation for female ornaments (Amundsen, 2000a, b), and until recently, little attention has been paid to sexual selection driving the evolution of female ornamentation (Amundsen, 2000b). Traditionally, the genetic correlation hypothesis has been a popular explanation for extravagant female traits (Lande, 1980, 1987). This hypothesis predicts that as sexual selection increases the size or expression of a male character, a similar response is seen in the female character because males and females share the same genes (Lande, 1980, 1987). While such genetic correlations exist, and can explain why females rarely express traits not expressed in males, this hypothesis does not exclude female ornaments from being subject to direct sexual selection. Price and Birch (1996) showed frequent changes from monochromatism to dichromatism (and visa versa) in passerine birds suggesting that color ornamentation in one sex is not constrained by ornamentation in the other, thus weakening the general explanation that female ornamentation is dependent on the expression of male ornamentation. It is important to note that the indirect selection that could be imposed through between-sex genetic correlations and sexual selection acting directly on females to drive the evolution of ornamentation are not mutually exclusive mechanisms. Hence, support for the genetic correlation hypothesis does not necessarily

contradict any evidence for sexual selection acting directly on the female phenotype. In light of this, Amundsen (2000a, b) states that in species where males and females express similar traits there is likely a genetic correlation, however selection can still act on female traits through either female-female competition or male mate preference.

Females often compete for access to reproductive resources such as nesting sites, mates, or both (Johnson, 1988; Jonart et al., 2007; West-Eberhard, 1983b). Female ornaments may be used in competition to signal dominance or quality to same-sex conspecifics (Hanssen et al., 2006), therefore selecting for females with traits linked to dominance. Evidence for this has been demonstrated in species with sex-role reversal, such as pipefish (*Nerophis ophidian*), in which females compete for males (e.g., Bernet et al., 1998). However, this phenomenon should not be limited to sex-role reversed species. Johnson (1988) demonstrated that in female pinyon jays (*Gymnorhinus cyanocephalus*), a socially monogamous bird with typical sex roles, head color correlated with dominance, and social rank was in turn, associated with mating success. Female house finches (*Carpodacus mexicanus*) often engage in aggressive encounters when another female invades their territory. Larger females in better condition typically win in these fights (Jonart et al., 2007). Additionally, Heinsohn and colleagues (2005) suggest that the female ornamentation found in *Eclectus roratus* parrots is a result of intra-sexual competition among females for nest cavities and food.

Male mate preference can also drive selection for female ornaments (Amundsen, 2000a; Bonduriansky, 2001). When there is variation in female quality and fecundity, it may benefit males to choose better quality or more fecund mates (Amundsen, 2000b; Burley, 1977; Servedio and Lande, 2006). Males would also benefit from being choosy

when they are investing in offspring through parental care, consequently lowering their potential reproductive output. There is ample empirical evidence that females prefer males with more elaborate characters such as color (e.g., Hill, 1990, 1991; Siefferman and Hill, 2003; Siitari et al., 2002) and long tails (Møller et al., 1998). However, in several monogamous species where males provide a significant amount of parental care, increasing their overall investment in the offspring, males should benefit by becoming choosier (Burley, 1977; Gowaty and Plissner, 1998). For example, in zebra finches (*Taeniopygia guttata*), socially monogamous, biparental birds, there is variation in female fecundity that relates to protein availability and condition (Houston et al., 1995; Selman and Houston, 1996) and males demonstrate a preference for the more fecund female (Jones et al., 2001; Monaghan et al., 1996).

Overall, there are a limited number of studies that have addressed the evolution of female ornamentation via male mate preference. Species in which males have demonstrated mate preference include rock sparrows (*Petronia petronia*) (Griggio et al., 2005), zebra finches (Burley, 1977; Jones et al., 2001; Monaghan et al., 1996), and bluethroats (*Luscinia s. svecica*) (Amundsen et al., 1997). Some of the earliest evidence came from crested auklets (*Aethia cristatella*) where mounts of males and females with large crests received more sexual displays from the opposite sex than mounts with small crests (Jones and Hunter, 1993). Unlike models of female preference and male ornaments where a preference for an arbitrary trait will persist (Kirkpatrick, 1996; Kirkpatrick et al., 1990; Lande, 1980), models of male mate choice predict that male preference cannot persist unless the preferred female traits signal fecundity or quality because the cost of choice appears to be higher for males (Ihara and Aoki, 1999; Servedio and Lande, 2006).

There is a growing body of evidence that demonstrates the relationship between ornament and individual and/or reproductive quality in females. More colorful female northern cardinals (*Cardinalis cardinalis*) appear to be better parents than duller females (Linville et al., 1998). Female pied flycatchers (*Ficedula hypoleuca*) with white forehead patches have fewer parasites than females without this patch (Potti and Merino, 1996). And female common eiders (*Somateria mollissima*) with larger wing bands lose less body mass during the breeding season and have higher immune cell levels making them more tolerant to the costs of reproduction (Hanssen et al., 2006). Siefferman and Hill (2005b) showed that the blue structural coloration of rump and tail plumage in eastern bluebirds (*Sialia sialis*) is a nutritionally-dependent trait. Females that were nutritionally stressed before and during molt grew significantly duller blue plumage than females on a normal diet (Siefferman and Hill, 2005b). This suggests that female coloration in eastern bluebirds may signal a female's ability to forage and indicate condition. In blue tits (*Cyanistes caeruleus*), the carotenoid-based yellow plumage and the structurally-based blue plumage were both positively linked to various metrics of reproductive success and individual quality which indicates that female coloration may be a sexually selected trait (Doutrelant et al., 2008).

Unfortunately, most studies fail to connect the mechanism (female-female competition or male mate preference) with the relationship between ornamentation and quality. While there is evidence that female coloration in barn swallows (*Hirundo rustica*) indicates reproductive quality (Safran and McGraw, 2004), no study has addressed whether this relationship is driven by sexual selection. Additionally, those studies that do attempt to describe both the female signal and the mechanism often fall

short of accomplishing this goal. Although male bluethroats prefer brighter females (Amundsen et al., 1997), female color does not correlate with female parental quality (Smiseth and Amundsen, 2000). These examples illustrate the need for more research on the function of female ornamentation and the role of sexual selection in driving and maintaining ornamentation. In this study we attempt to connect the mechanism with a female ornament where there is evidence that sexual selection is operating directly on female plumage variation.

Eastern bluebirds are socially monogamous birds that exhibit biparental care. They are also sexually dimorphic and dichromatic. Males have bright blue plumage over most of their back, wings, tail, and head and chestnut plumage on their breast (Siefferman and Hill, 2003). Females possess similar traits and there is substantial among-individual variation in both sexes (Siefferman and Hill, 2003, 2005b), however females are more drab than males in regards to both blue and chestnut coloration. In males, coloration is a sexually selected trait; males with brighter blue plumage and darker chestnut plumage experience higher reproductive success, pair with females that initiate nests earlier, and provision incubating females at a higher rate (Siefferman and Hill, 2003). While there is some evidence that female bluebird coloration correlates with various fitness metrics such as clutch initiation date, maternal provisioning rate, and offspring condition (Siefferman and Hill, 2005b), there is no published evidence that sexual selection is acting on female traits through either male preference or female-female competition.

The goal of this study was to investigate the function of female coloration in eastern bluebirds. First, I compared female coloration with individual and reproductive quality. These traits may indicate quality to potential mates and to other females in

competition for mates or reproductive resources. Second, I determined if male mate preference currently selects for variation in female coloration. I hypothesized that more colorful females (i.e., females with brighter and bluer rumps and/or darker and redder chests) would have greater mating and reproductive success indicated by a shorter latency to clutch initiation, larger egg volume, greater chick condition, and a larger number of fledglings. Additionally, if female coloration is a trait selected for via male mate preference, I hypothesized that males would prefer to associate with more colorful females in experimental mate preference trials.

Methods

Study System

I studied free-living and captive populations of eastern bluebirds (*Sialia sialis*) in Williamsburg, James City and York Counties, Virginia. In this area, eastern bluebirds are found year (Gowaty and Plissner, 1998). They are secondary cavity nesters; therefore, nesting sites are a limiting resource and they will readily use manmade nest boxes (Gowaty and Plissner, 1998). There is a network of 500-600 nest boxes throughout the study area with an established, marked population of breeding bluebirds that we have been studying in detail since 2003. Once paired, females will build a nest; the first nest can take up to three weeks to complete. Once the nest is complete, females will begin laying eggs; females lay one egg a day with clutch sizes ranging from three to seven with a modal clutch size of five (Gowaty and Plissner, 1998). Females typically begin incubating the day the last egg is laid and the incubation period is approximately 14 days.

Chicks generally hatch synchronously and stay in the nest for 18 days. Birds in our population will readily double brood, and occasionally third clutches are laid.

Field studies

I conducted fieldwork from late February through early August in 2007 and late March through June in 2008. Specifically, I focused my efforts on the first clutches in both the 2007 ($n = 41$) and 2008 ($n = 79$) breeding seasons. Nest boxes were monitored weekly until the beginning of egg-laying. Once egg-laying had been completed, I recorded clutch size and average egg volume. Egg volume was determined by measuring the width at the widest part (breadth) of the egg and the length at the longest point with plastic dial calipers to 0.1 mm precision. I used Hoyt's equation to determine egg volume:

$$V = 0.51 * L * B^2$$

where L is the maximum length and B is the maximum breadth (Hoyt, 1979).

I continued to check nests weekly until hatching at which point I recorded brood size. During the nestling stage, I captured the adults (in 2007 females $n = 41$, males $n = 35$; in 2008 females $n = 79$, males $n = 68$) using trapdoor nest-box traps (Stutchbury and Robertson, 1986). At the time of capture, adults were banded with a numbered aluminum US Geological Survey band and a unique combination of three plastic color bands. At this time, I sampled from three plumage patches by plucking a small number of feathers for later spectrometric analyses: the outer two retrices of the tail, nine or more feathers from the chest patch, and nine or more feathers from the rump patch. Feathers taken from the chest and rump patch were all taken from the same area of the patch on either the left or the right side of the bird (randomly determined). Additionally, I collected the

following morphological data: body mass (with an electronic balance to 0.1 g precision) and unflattened wing chord (with dial calipers to 0.1 mm precision). These data were typically collected during the first five hours after dawn. In the 2008 season, in addition to feather samples and morphological measurements, I collected blood samples from every adult bird for genetic parentage analyses, which I do not report here.

Approximately 100 μ l of blood were taken via brachial vein puncture.

On day 12, nestlings were banded, and we recorded body mass and wing chord using the same techniques as for the adult sampling. We also collected blood samples from nestlings in 2008. The number of nestlings on day 12 was assumed to be the number of nestlings fledged unless there was evidence to the contrary. Our previous years of data indicate that this assumption is appropriate (J. P. Swaddle, unpublished data). Our metrics of reproductive success were correlated within a nest; therefore we used principal components analysis (PCA, employing the correlation matrix method) to combine clutch size, average egg volume, brood size, average chick condition, and number of fledglings. PC1 loaded positively and heavily for clutch size, brood size and number of fledglings, while PC2 loaded positively and heavily for average egg volume and brood condition (Table 1).

At a subsample of 45 nests I conducted 60-minute behavioral observations ($n = 17$ in 2007, $n = 28$ in 2008) during the nestling stage in order to quantify provisioning rate by the adults. In 2007, these observations were performed when the nestlings were 5 days and 12 days post-hatching. As nestlings were generally still being brooded by the female on day 5, I subsequently dropped those observations from all analyses and used the 12-day provisioning data only. In 2008, I conducted observations only on day 12. During

observations, I recorded the number of trips to the nest box and the time spent in the nest box (seconds). If a bird went to the nest box, but did not enter the box, the time in the nest box was recorded as 0 seconds, but was still recorded as a trip because at day 12, the chicks are big enough to be fed without completely entering the box.

Body Condition

Body condition is defined as mass corrected for body size. Adult body condition was the residuals of mass regressed over wing using a linear regression. Due to sexual size dimorphism, we conducted regressions separately for males and females. The growth curve for nestlings is not linear; therefore, nestling condition was the residuals of mass regressed over wing using a cubic regression. Nestling condition early in the nesting stage is highly correlated to condition later in the nesting stage. Therefore, for nests where nestlings died or were depredated before day 12, we used earlier measurements when available. We averaged nestling condition within a brood to achieve a measure of brood condition.

Plumage Color Analysis

Feather samples were stored in sealed envelopes at room temperature. Feather color analyses followed a protocol similar to Siefferman and Hill (2003). For rump and chest patches, nine feathers were arranged on a standard black card background in a similar manner as the feathers overlap on the body of a bird; each tail feather was analyzed individually against the same black background. Feather samples were analyzed with an Ocean Optics USB2000 spectrometer (range 200-1100 nm) using a fiber optic probe at an

angle of 90° to the feather surface lit by a PX-2 pulsed xenon light source. Ambient light was excluded using a metal probe holder, which was placed against the feather sample; and held the probe at a constant distance so that a 3 mm diameter of light hit the feather surface.

Reflectance data were generated relative to a white standard (Ocean Optics WS-1) and a dark standard (all light excluded). Spectra were recorded with OOIrrad, a spectra acquisition software package produced by Ocean Optics. For each sample, 20 spectra were averaged to reduce noise from the spectrometer with an integration period of 100 ms. This procedure was repeated three times for each sample with the probe lifted between each scan. The three scans were of three different locations (center, right of the rachis, and left of the rachis) in the colored area of the feather in order to get an average of the overall color of that sample.

The first step in analyzing color was to quantify the standard descriptors: hue, brightness, and chroma. Hue is the wavelength at the maximum reflectance (λ_{Rmax}), brightness is the amount of light reflected by the feather surface between 300 and 700 nm, and chroma is the percentage of the total reflectance within a particular color range: 300-400 nm for UV and 600-700 nm for red (Siefferman and Hill, 2003). Due to the differences in reflectance properties, the steps for quantifying hue and chroma were different for the structurally-based and the melanin-based colors (Siefferman and Hill, 2003). For the blue structurally-based color, hue is the wavelength at maximum reflectance (λ_{Rmax}) and chroma is the reflectance in the UV color range (300 nm-400nm) divided by the total spectral range (300 nm-700nm) (Montgomerie, 2006; Siefferman and Hill, 2003). For the chestnut melanin-based color, the spectral curve is still increasing at

700 nm; therefore hue is the wavelength where the slope of the curve is the greatest (Siefferman and Hill, 2003) and chroma is the reflectance in the red color range (600 nm-700 nm) divided by the total spectral range (300 nm-700 nm) (Montgomerie, 2006; Siefferman and Hill, 2003). Within a plumage patch, these color descriptors are correlated, therefore, we ran PCA, separately for each patch, to reduce the number of variables. PCs were generated from female plumage; we then used the loadings from the female PCs to generate male PCs for within-pair color comparisons.

Principal Components Analysis of Natural Plumage Coloration

We ran PCA for the three plumage patches using the color descriptors described previously (brightness, hue, and chroma – UV or red). Female chest coloration yielded one PC, with an eigenvalue greater than one, which explained 60.1% of the variance in the data (Table 2). Female chest PC1 loaded positively for hue and red chroma and negatively for brightness. Females with a high chest PC1 scores had darker, redder chest plumage. Female rump coloration yielded two PCs that explained 94.8% of the variance in the data (Table 3). Female rump PC1 loaded positively for UV chroma and negatively for hue, thus females with a high rump PC1 score had bluer, more UV-rich rump plumage. Female rump PC2 loaded positively for brightness and somewhat positively for hue. Hence, females with a high rump PC2 score had brighter plumage that was slightly less blue (i.e., longer wavelengths of light reflected). The female tail coloration PCA yielded one component that explained 59.9% of the variance in the data (Table 4). Female tail PC1 loaded positively for UV chroma, negatively for hue, and somewhat positively for brightness. Therefore, females with a high tail PC1 score had retrices with

more UV-rich reflectance that were slightly brighter in general. From the female PC loadings and eigenvalues of components, we generated male PC scores for within-pair comparisons.

Statistical Analyses of Field Data

We analyzed data from 2007 and 2008 together. For females caught in both years, we randomly chose one year to include in analyses, which altered the sample sizes in these analyses (2007: females $n = 35$, males $n = 29$; 2008: females $n = 72$, males $n = 66$). We tested for normality using Shapiro-Wilk tests and used parametric tests only when the assumption of normality was met. We square-root transformed date on first egg date. We explored how metrics of female mating and reproductive success could be explained by female coloration using multiple regression models. We tested for evidence of assortative mating by condition and coloration using Spearman's rank correlations. We computed all statistics using SPSS (v. 15.0 for Windows). All computation of color descriptors was performed using the *R* statistical programming package (v. 2.6.0) (<http://www.r-project.org>).

Male Mate Preference

For the captive study, I captured males and females from a different part of the study population than was used for field studies. Birds were housed in an outdoor aviary for mate choice trials (males $n = 12$, females $n = 12$). Cages were 2.5 x 3 x 3 m and partitions with 1 x 1 cm galvanized hardware cloth. Females were caught using trapdoor nest-box traps during the nest-building stage and male were caught using a mist net with playback

and a decoy, both during the nest-building stage. I experimentally altered color patches (within the natural range) of the females (increasing/decreasing brightness of rump and darkening/lightening chest patches) in a factorial manner using a repeated-measures design. This yielded four female treatments: (1) bright rump and dark chest, (2) bright rump and light chest, (3) dull rump and dark chest, and (4) dull rump and light chest.

Upon capture, the twelve stimulus females were randomly assigned to one of four treatment groups with three females in each group. Plumage patches were fully colored according to treatment group with non-toxic, permanent Prismacolor[®] or Sharpie[®] markers (bright rump: Prismacolor[®] violet mist; light rump: Sharpie[®] black; dark chest: Prismacolor[®] light tan; light chest: Prismacolor[®] buff). Touch ups were made as needed one day prior to when a female was used in a mate choice trial; typically every other week (Fig. 1). The chest plumage treatments achieved the desired result of increasing and decreasing brightness; however, both rump treatments decreased brightness overall. Despite that, on average females in the bright rump treatment still had brighter rumps than females in the dull rump treatment.

The twelve males experienced six pair-wise mate preference trials of approximately two hours each. Each trial offered the male a preference between unique combinations of the four female treatments (six possible combinations for pair-wise presentation of the four treatments), yielding a total of 72 preference trials for the entire experiment. Before each trial a female from the appropriate treatment group was randomly assigned to the trial. By randomly assigning females for each trial, I minimized the effects of among-female morphological and behavioral differences that may influence male preference.

All mate preference trials were conducted in a large mate preference aviary (Fig. 2). In this aviary, the two stimulus females were placed in the outer two cages approximately 10 meters from one another. The male was placed in the area between the females, which consisted of four connected cages. The central two cages were considered a neutral area; when the male was in this area, we assumed the male was not exhibiting a preference. When the male was in either of the outer two cages of their area (i.e., the areas adjacent to each of the female stimulus cages) we considered that males could be exhibiting a preference for the nearest female. There was an area with artificial turf and a nest box in these preference areas to stimulate courtship activities. I placed an excess of perches evenly throughout all male and female cages. During trials, I video recorded both males and females (with a Sony[®] handycam HDR-SR1) to assess male preference and partition out female behavioral changes that may be a result of the plumage manipulations. I assumed that male preference increased when the following behaviors were exhibited in front of each female: time spent in a preference cage, the number of songs directed at a female, number of displays directed toward a female, and number of box visits (Amundsen et al., 1997; Swaddle et al., 2005; Swaddle and Cuthill, 1994). These behaviors were positively correlated; therefore we reduced them to one variable using PCA (Table 5).

Statistical Analyses for Male Mate Preference Trials

We averaged each male's preference score for each female treatment and used repeated-measures ANOVA to determine whether male preference differed between the four female treatment groups. We computed all statistics using SPSS (v. 15.0 for Windows).

Results

Female Coloration and Quality

We used linear regression to explore relationships between female coloration and body condition measured during the nestling stage. Female body condition was not significantly predicted by chest coloration ($R^2 = -0.011$, $F_{1,91} < 0.01$, $p = 0.999$), rump coloration (PC1: $R^2 = 0.010$, $F_{1,105} = 2.065$, $p = 0.154$; PC2: $R^2 = -0.009$, $F_{1,105} = 0.011$, $p = 0.916$), or tail coloration ($R^2 = -0.008$, $F_{1,102} = 0.181$, $p = 0.671$).

We constructed multiple regression models to explore relationships between female coloration and metrics of reproductive quality: latency to clutch initiation, reproductive quality PC1 (clutch size, brood size, and number of fledglings), and reproductive quality PC2 (average egg volume and brood condition). We included year, female body condition, female tail PC1, female rump PC1, female rump PC2, and female chest PC1 as predictors. Latency to clutch initiation was not significantly predicted by the model ($R^2 = -0.007$, $F_{6,83} = 0.900$, $p = 0.499$; Table 6). Reproductive quality PC1 was weakly predicted by the model ($R^2 = 0.058$, $F_{6,73} = 1.911$, $p = 0.109$; Table 7), with tail color being the only predictor which was significantly related to this fitness metric (Table 7). Females with tails that were more reflective in the UV spectrum tended to have larger clutches, larger broods, and fledge more offspring from their nests.

Reproductive PC2 was significantly predicted by the model, but the pattern was only marginally significant ($R^2 = 0.086$, $F_{6,73} = 2.243$, $p = 0.048$; Table 8). Of the individual predictor variables, female condition was the best predictor of reproductive quality PC2 and tail color PC1 was also weakly indicative of this fitness metric (Table 8).

Overall, females in greater body condition and with tails that were more reflective in UV colors tended to lay larger eggs that resulted in broods in better body condition.

We also constructed multiple regression models to assess the relationships between female coloration and the proportion of female feedings/chick/hour, as an index of maternal effort. Using the same predictors, the model did not predict variation in maternal feeding rates ($R^2 = 0.009$, $F_{6,33} = 1.059$, $p = 0.407$; Table 9).

Assortative Mating

We found evidence consistent with assortative mating by body condition and by tail coloration in that, within pairs, male and female body condition ($r_s = 0.275$, $n = 93$, $p = 0.008$; Figure 3) and tail coloration ($r_s = 0.247$, $n = 91$, $p = 0.018$; Figure 4) were positively correlated. However, there were no significant male-female correlations in chest or rump coloration (chest PC1: $r_s = 0.138$, $n = 80$, $p = 0.222$; rump PC1: $r_s = -0.023$, $n = 94$, $p = 0.825$; rump PC2: $r_s = 0.087$, $n = 94$, $p = 0.404$).

Male Mate Preference

All twelve males showed apparent mating interest in stimulus females in the aviary preference trials. Males readily moved throughout the entire preference chamber and typically associated with both females and displayed sexual behaviors: singing, wing-waving display, and visiting/entering the nest box. There was no difference in our multivariate index of male preference between female color treatments ($F_{3,8} = 0.418$, $p = 0.745$; Figure 5). Because the preference trials spanned a period of two months during the breeding season and we suspected that males' sexual interest in females could vary over

this time, we included trial date as a covariate in a further repeated-measures ANOVA; Date had little effect on our interpretation ($F_{3,8} = 0.306, p = 0.821$). There were three males that, in one or more trials, did not leave the neutral area of the preference chamber. Excluding these males from the analyses did not qualitatively alter the overall results.

Discussion

We found that females in better condition and with bluer tails had higher reproductive success. These females tended to lay larger eggs and produce broods in better condition. Additionally, females with bluer tails tended to have a higher reproductive output in terms of clutch size, brood size, and number of fledglings. This suggests that females in better condition can lay larger eggs and feed nestlings more efficiently. Body condition is likely a result of the territory or habitat in which a female is breeding. Females residing in territories with an abundant food source will, themselves, be in better condition, and consequently, also have the resources to produce quality eggs and provide a sufficient amount of food to nestlings. Blue coloration of tails, however, is not related to current condition as color is established several months prior to arrival on the breeding grounds. Therefore, tail color may be a signal to potential mates of a females' reproductive quality. Additionally, the weak relationship between tail color and reproductive output suggests that tail color may be an indicator of fecundity. Males can use tail coloration to assess a females' overall reproductive quality; females with bluer tails produce more young and young in better condition and as a result, may be more attractive to males.

Interestingly, our results also suggest that assortative mating by adult body condition and tail color could be occurring. A possible explanation for assortative mating

by body condition is that within a pair, males and females are sharing the food resources of their territory, and as a result, are both in similar condition. Tail coloration, however, is not determined by the current habitat. Eastern bluebirds molt in late summer/early fall (Gowaty and Plissner, 1998), and excluding wear (Gunderson, 2008), tail coloration is a relatively static trait. Therefore, tail coloration may be a trait used in mutual mate choice. Males that choose females with bluer tails will likely have a higher reproductive success, and females that choose males with bluer tails will receive more male provisioning rates to females during incubation and a greater parental investment (Siefferman and Hill, 2003, 2005a).

In a similar study, Siefferman and Hill (2005b) also found that female coloration in eastern bluebirds in Auburn, Alabama may be an indicator of reproductive success. As with our study, they found that female condition and tail coloration relate to offspring condition. However, there appears to be geographical variations in regards to the relationships between female coloration and latency to clutch initiation and number of fledglings. In the Siefferman and Hill (2005b) study, latency to clutch initiation was also related to female tail coloration and body condition, whereas in our study, female chest coloration appeared to be the best predictor of the date a female laid her first egg. In the Alabama population female coloration of any plumage patch failed to predict the number of fledglings produced, and in our Virginia population, female tail coloration was a weak predictor of reproductive output. In our study, we had a very small sample of birds that we knew the exact age of and consequently, age was not included in our models. However, female age was a predictor of several metrics of reproductive success in the Alabama population; consequently, this may account for the discrepancies between the

two studies. However, when we constructed backwards stepwise regression models (as in Siefferman and Hill, 2005b) using the same predictors (excluding age), the final models for latency to clutch initiation and number of fledglings shared none of the same predictors, even weak predictors. Seifferman and Hill found that female tail coloration, female age, and female condition were significant predictors of the date of first egg, and date of first egg, female age, and female condition were significant predictors of the number of fledglings. However we found female chest coloration to be the only significant predictor of date of first egg, and male rump and chest coloration, and female tail coloration to be significant predictors of the number of fledglings. Differences in field techniques and photospectrometry equipment seem insufficient to cause such marked differences between populations, therefore there may be some degree of geographic variation in the function of female coloration or the mechanisms driving that variation.

Despite the apparent relationship between female coloration and reproductive success, we found no evidence of male mate preference in a controlled aviary experiment. However, in our experiment we were explicitly testing whether female chest and rump brightness influenced male preference. Tail coloration was not manipulated or considered in this experiment because tail plumage of captive birds was extremely worn after a short period of time in captivity. Additionally, tail coloration in terms of tail PC1 accounts mostly for variation in hue and UV chroma (blueness), and less for variation in brightness. However, the plumage treatments of females in the preference trials differed in brightness more than any other color descriptor. Consequently, the preference trials may not have accurately tested male preference for variation in coloration. Additionally, preference trials took place between May and July; males were captured defending nest

boxes and had already formed a pair bond. The intensity of sexual behaviors appeared to decrease over the time period we ran trials (J. K. Hubbard, personal observation).

Consequently, future studies of male preference should attempt to assess preference at the time of pair formation rather than throughout the breeding season. Additionally, future studies should explore the influence of variation in all color characteristics on preference.

The goal of this study was to determine the function of female coloration by assessing the relationship between coloration and reproductive success while also testing whether male preference for colorful females is selecting for variation in female coloration. Female body condition and tail coloration both related to metrics of reproductive success. In our study, we concentrated on first broods because there are different costs associated with second clutches, such as laying more eggs and energetic costs of raising a second brood. However, studies have shown that variation in female coloration may indicate a female's ability to overcome these costs (e.g., Doutrelant et al., 2008; Safran and McGraw, 2004). Because sexual selection operates on variation in mating and reproductive success, it is important to consider mating and reproductive success throughout an entire breeding season, perhaps even lifetime. Our study, with its limitation to first broods, cannot, at this time, demonstrate relationships between female coloration and reproductive success of an entire breeding season, although, we have data available to perform such an analysis in the future.

The second part of our study explored the influence of female coloration on male preference. We found no evidence that female rump and chest coloration influenced male preference. However, given the timing of our experiments we were testing preferences throughout the breeding season, rather than preferences at the time of pair formation.

Throughout the breeding season, both males and females engage in extra-pair copulations (EPC), however there is some debate about whether males solicit females, or females solicit males. The high rate of extra-pair young in birds, more than 10% within a clutch (Griffith and Montgomerie, 2003), has spurred the idea that females gain some indirect genetic benefit by engaging in EPCs (Jennions and Petrie, 2000; Kempenaers et al., 1992). In this vein, female coloration may be important in attracting extra-pair males. However, Arnqvist and Kirkpatrick (2005) demonstrate that the potential indirect benefits females gain via EPCs is not enough to offset the loss of direct benefits, such as parental care, from the social mate. Consequently, female coloration may represent a balance between attracting a social mate at the start of the breeding season and avoiding the attention of coercive extra-pair males throughout the breeding season. We saw no influence of female coloration on male preference, however, because our experiment took place after the time of pair formation, our results could indicate that males have no preference for colorful extra-pair mates. Instead, extra-pair matings are opportunistic, or even coercive, resulting in a lack of male preference throughout the breeding season.

Mate preference and competition are the two classical mechanisms of sexual selection. Our aviary experiment indicates that male preference for rump and chest color does not appear to drive variation in these female plumage patches in eastern bluebirds. However, tail coloration does provide some information about reproductive quality of an individual. The lack of male preference for female rump and chest colors does not preclude female tail coloration from being a sexually selected trait. Additionally, we did not investigate the possible role of female-female competition driving selection for differential coloration in female eastern bluebirds. In male eastern bluebirds, the UV-blue

coloration of their head, back, tail, and wings are predictive of competitive ability and males with more UV chroma settle in a territory before males with less UV chroma (Siefferman and Hill, 2005c). Additionally, in aviary preference trials, female eastern bluebirds show no preference for males with more elaborate blue coloration (Liu et al., 2007). During the breeding season, both males and females will aggressively defend their territory and nest box from intruding conspecifics (Gowaty and Plissner, 1998). Consequently, it is possible that variation in female coloration is also driven by within-sex competition. Given that both males and females show no preference for more colorful mates, competition within both sexes for territories and other reproductive resources could explain the assortative mating by tail coloration we found in this study. If female coloration, as with male coloration, is predictive of competitive ability, the bluest males and the bluest females could be outcompeting rivals for the most desirable territories. As a result, the most desirable territories are settled by pairs that both possess the bluest tails, and the least desirable territories are settled by birds with duller, less blue tails. A thorough examination of female coloration and competitive ability in eastern bluebirds is needed to determine the likelihood of this explanation.

In conclusion, sexual selection does not appear to be currently acting on rump and chest coloration of female eastern bluebirds. The coloration of these two patches is not related to reproductive success and does not influence male mate preference. However, tail coloration weakly predicts reproductive success and may be a sexually selected trait. Yet the mechanisms driving selection are still unknown; a direct test of male preference for female tail coloration is needed. Additionally, a test of male mate preference during pair formation will provide a better test of male preference for female coloration. Female-

female competition is an attractive alternative to mate preference, especially given the selective forces for male coloration. Our findings, along with other recent studies, indicate that female coloration can serve as an indicator of reproductive success and further investigation of the mechanisms driving the evolution of female coloration are needed to truly understand the evolution of female ornamentation.

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Table 1: Principal component loadings for reproductive quality metrics (cumulative variance explained in parentheses).

	PC1 (36.6%)	PC2 (58.7%)
Clutch Size	0.740	0.083
Average Egg Volume	-0.193	0.704
Brood Size	0.874	0.090
Brood Condition	-0.248	0.721
Number of Fledglings	0.647	0.270

Table 2: Principal components loadings for female chest color scores (cumulative variance explained in parentheses).

	PC1 (63.1%)
Brightness	-0.899
Hue	0.654
Red Chroma	0.828

Table 3: Principal component loadings for female rump color scores (cumulative variance explained in parentheses).

	PC1 (60.0%)	PC2 (34.7%)
Brightness	0.378	0.916
Hue	-0.858	0.449
UV Chroma	0.960	0.041

Table 4: Principal component loadings for female tail color scores (cumulative variance explained in parentheses).

	PC1 (59.9%)
Brightness	0.433
Hue	-0.852
UV Chroma	0.941

Table 5: Principal component loadings for male preference behaviors (cumulative variance explained in parentheses)

	PC1 (64.5%)
Number of Songs	0.923
Number of Displays	0.846
Number of Box Visits	0.725
Time with Female	0.696

Table 6: Multiple regression model for latency to clutch initiation ($R^2 = -0.007$, $F_{6,83} = 0.900$, $p = 0.499$).

Predictors	Beta	t	p
Year	-0.007	-0.060	0.952
Female Condition	-0.064	-0.588	0.558
Female Tail PC1	-0.112	-0.927	0.357
Female Rump PC1	0.030	0.263	0.793
Female Rump PC2	-0.035	-0.324	0.747
Female Chest PC1	-0.240	-2.118	0.037

Table 7: Multiple regression model for reproductive quality PC1 ($R^2 = 0.058$, $F_{6,73} = 1.91$, $p = 0.109$).

Predictors	Beta	t	p
Year	-0.073	-0.604	0.548
Female Condition	0.056	0.504	0.616
Female Tail PC1	0.281	2.296	0.025
Female Rump PC1	-0.026	-0.227	0.821
Female Rump PC2	-0.159	-1.442	0.154
Female Chest PC1	-0.083	-0.718	0.475

Table 8: Multiple regression model for reproductive quality PC2 ($R^2 = 0.086$, $F_{6,73} = 2.243$, $p = 0.048$).

Predictors	Beta	t	p
Year	0.119	1.002	0.319
Female Condition	0.306	2.779	0.007
Female Tail PC1	0.232	1.927	0.058
Female Rump PC1	-0.157	-1.372	0.174
Female Rump PC2	0.139	1.278	0.205
Female Chest PC1	0.052	0.453	0.652

Table 9: Multiple regression model for maternal feeding rate ($R^2 = 0.009$, $F_{6,33} = 1.059$, $p = 0.407$).

Predictors	Beta	<i>t</i>	<i>p</i>
Year	0.225	1.229	0.228
Female Condition	-0.049	-0.293	0.772
Female Tail PC1	-0.229	-1.316	0.197
Female Rump PC1	0.076	0.464	0.646
Female Rump PC2	0.140	0.860	0.396
Female Chest PC1	-0.133	-0.910	0.424

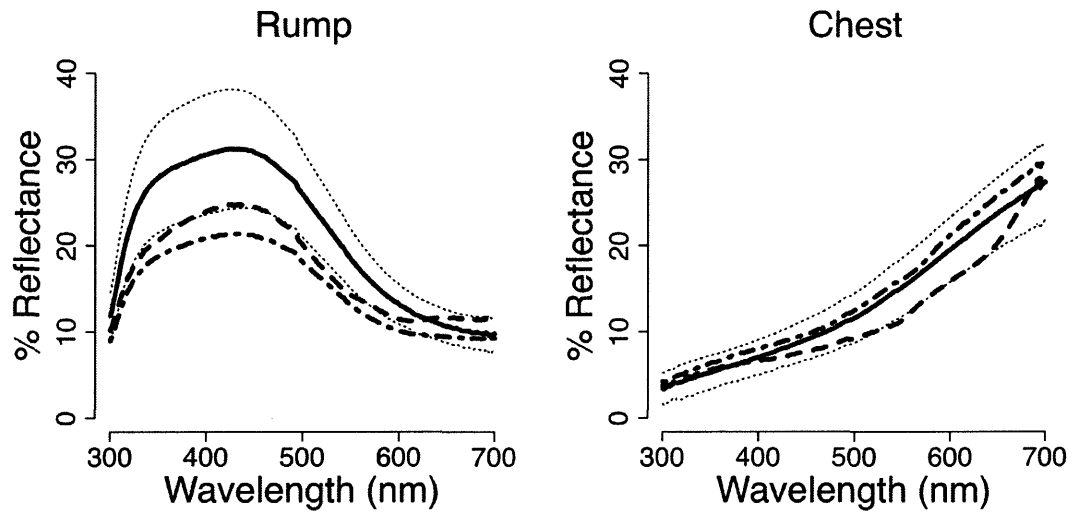


Figure 1. Reflectance spectra showing the effect of rump and chest plumage manipulation for male mate preference trials. On both graphs the solid black line is the mean natural coloration ± 1 standard deviation (dotted lines), the dashed black line is the enhanced manipulation, and the dot-dashed black line is the reduced manipulation.

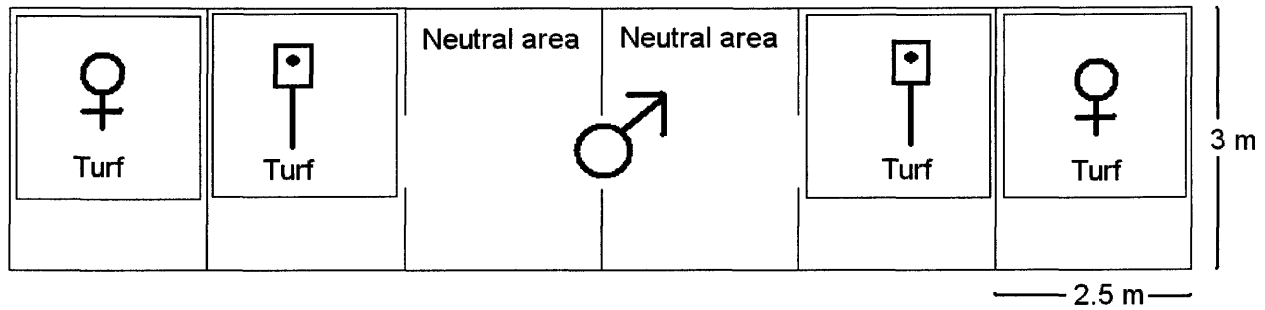


Figure 2. Plan view of the mate preference chamber. For each preference trial, a test male occupied the four central cages, which were open to each other. The two stimulus females occupied the outer cages and did not have physical access to the male. Male and females had access to artificial turf and the test male also had one nest box in each of the two cages that were closest to females. There were perches evenly dispersed throughout all cages. All cages were approximately 3 m tall.

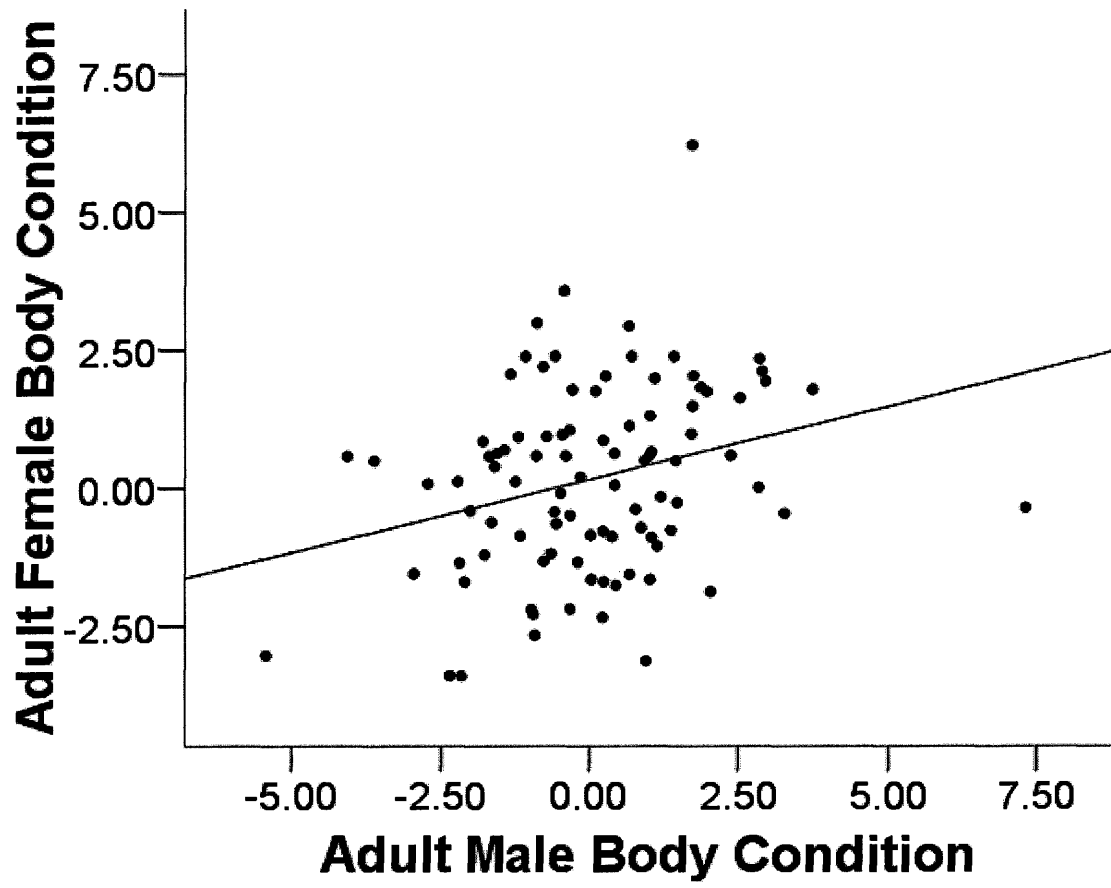


Figure 3: Positive association between adult body condition of males and females within breeding pairs.

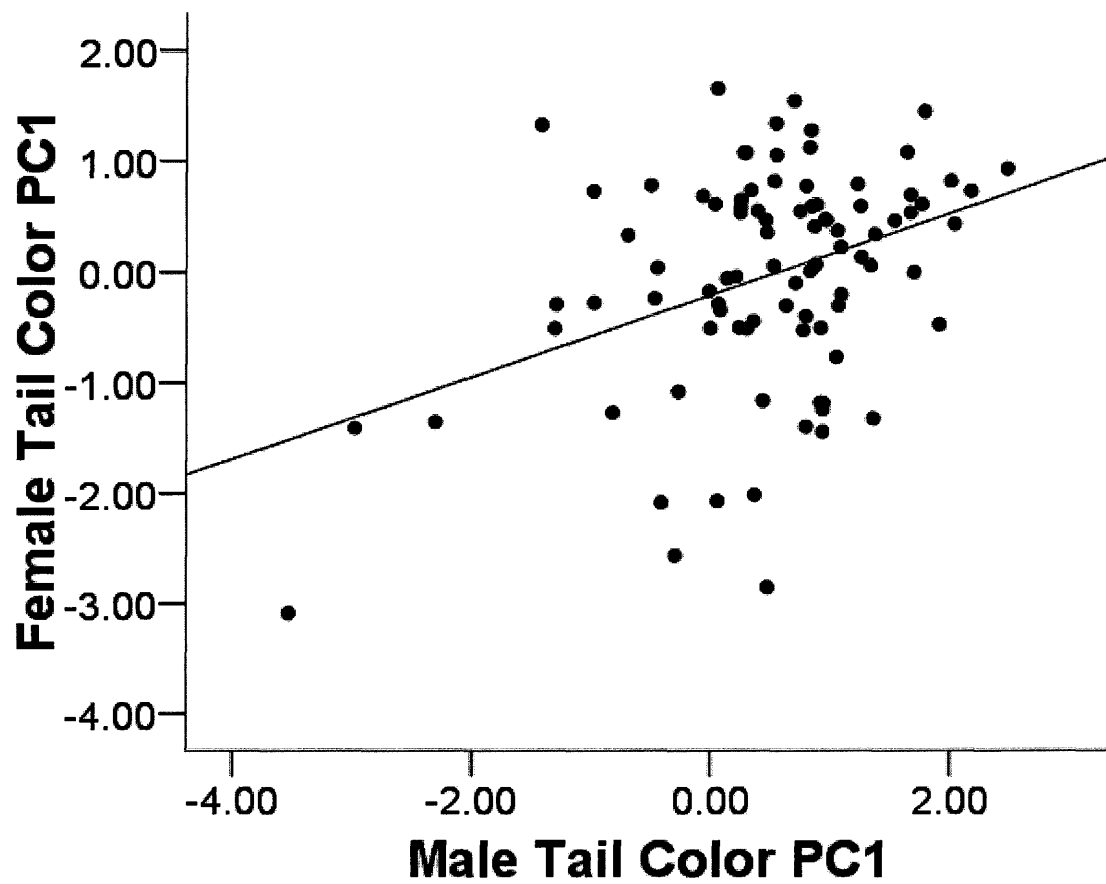


Figure 4: Positive association between adult tail coloration of males and females within breeding pairs.

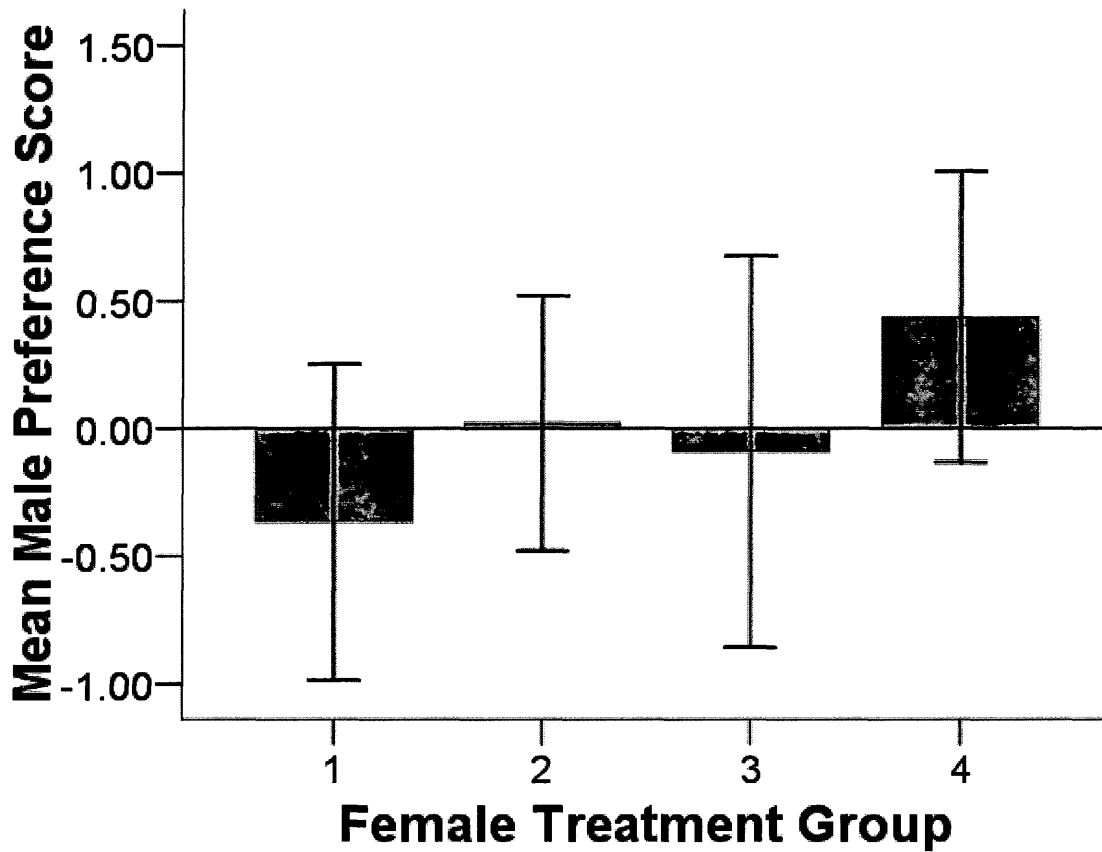


Figure 5: Mean (\pm SE) preference score (male preference PC1) displayed by males in front of each female color treatment group in the aviary preference trials (1: bright rump and dark chest, 2: bright rump and light chest, 3: dull rump and dark chest, 4: dull rump and light chest). There was no effect of female color on male preference.

Joanna Kay Hubbard

College of William and Mary

Education

The College of William & Mary Williamsburg, VA

M.S., Biology (2006-08)

Advisor: John P. Swaddle

“Female plumage coloration in eastern bluebirds, *Sialia sialis*: Is it a sexually selected trait?”

The University of Arizona Tucson, AZ

B.S., Ecology & Evolutionary Biology (2000-04)

Fellowships and Awards

Presidential Award for Excellence - Four year tuition waiver from the University of Arizona

UA Achievement Scholarship - Four year scholarship: \$500 per semester

Graduated *Cum Laude* from the University of Arizona

Phi Eta Sigma Honors Fraternity

Golden Key National Honour Society

Arts & Science Research Grant, College of William & Mary

Virginia Society of Ornithology; J. J. Murray Award

Coastal Virginia Wildlife Observatory Student Research Award

Williamsburg Bird Club Student Research Award

Graduate Studies Merit Fellowship, College of William & Mary

Outstanding TA prize, College of William & Mary

Research Experience

The College of William and Mary

Advisor: John Swaddle

Williamsburg, VA

“Female plumage coloration in eastern bluebirds, *Sialia sialis*: Is it a sexually selected trait?” (Aug 2006-August 2008)

Florida Fish and Wildlife Conservation Commission

Advisor: Karl Miller

Gainesville, FL

Monitored endangered Florida scrub jay population (Feb 2006-Jul 2006)

Emory University

Advisor: Donna Maney

Atlanta, GA

Captured White-throated Sparrows for behavioral/neuroscience study (Nov 2005-Jan 2006)

Huntsman Marine Science Centre

Advisor: Tracey Dean

St. Andrews, NB

Migration banding (Aug 2005-Oct 2005)

USGS/Colorado Plateau Research Station/Northern Arizona University

Advisor: Eben Paxton Roosevelt, AZ
Monitored endangered Southwestern willow flycatcher population (Apr 2005-Aug 2005)

Institute for Bird Populations

Advisor: Dave DeSante Little Rock, AR
Monitored over-winter survival of various sparrow species (Oct 2004-Mar 2005)

Smithsonian Environmental Research Center

Advisor: Peter Marra Edgewater, MD
Examined the effects of lead on nestling fitness/survival across a rural to urban gradient (May 2004-Sep 2004)

The University of Arizona

Advisor: Alex Badyaev Tucson, AZ
Assisted with various projects involving House Finches: coloration, mate choice, extra-pair paternity, etc (Sep 2003-May 2004)

Teaching Experience

College of William & Mary, Department of Biology

Williamsburg, VA
Principles of Biology: Molecules, Cells, and Development
Teaching Assistant
Responsible for teaching the lab component of the course. Updated and revised existing lab assignments (Jan 2008-May 2008).

College of William & Mary, Department of Biology

Williamsburg, VA
Integrative Biology: Animals
Teaching Assistant
Responsible for teaching the lab component of the course (Aug 2007-Dec 2007)

College of William & Mary, Department of Biology

Williamsburg, VA
Principles of Biology: Molecules, Cells, and Development
Teaching Assistant
Responsible for teaching the lab component of the course (Jan 2007-May 2007)

College of William & Mary, Department of Biology
Williamsburg, VA
Principles of Biology: Evolution and Ecology
Teaching Assistant
Responsible for teaching the lab component of the course (Aug 2006-Dec 2006)

University of Arizona, Department of Ecology and Evolutionary Biology
Tucson, AZ
Marine Discovery
Outreach Mentor
Responsible for providing demonstration to visiting elementary school students (Jan 2004-May 2004)

Presentations

Hubbard, JK and Swaddle, JP (International Society of Behavioral Ecology, 2008) Fancy females: the function of female coloration in eastern bluebirds, *Sialia sialis*.

Hubbard, JK and Swaddle, JP (College of William & Mary Graduate Research Symposium, 2008) Male mate choice and the function of female coloration in eastern bluebirds, *Sialia sialis*.

Hubbard, JK and Swaddle, JP (American Ornithologists' Union, 2007) Male mate choice based on sexually selected traits in female eastern bluebirds, *Sialia sialis*.

Hubbard, JK and Swaddle, JP (Animal Behavior Society, 2007) Female coloration, sexual selection, and male mate choice in eastern bluebirds, *Sialia sialis*.

Hubbard, JK and Swaddle, JP (College of William & Mary Graduate Research Symposium, 2007) Choosy males chose who? Exploring male mate choice in eastern bluebirds (*Sialia sialis*).

Professional Societies

Animal Behavior Society
American Ornithologists' Union
AAAS