Plumage as a Measure of Quality in Eastern Bluebirds

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ABSTRACT

The males of many animal species use bright colors and ornaments to attract potential mates. In this paper I examined studies of how plumage color in eastern bluebirds (*Sialia sialis*) affects mate choice. I compared findings on this species with findings on European starlings, zebra finches, and blue grosbeaks to identify which visual cues are commonly used by songbirds to identify possible mates. I found that plumage color in all four of these species was linked to individual health, offspring quality, and reproductive fitness. Two ideas that remain unknown are exactly how these visual cues evolve, and how birds learn to assess potential mates.

INTRODUCTION

Many species of male songbirds sing to attract females, but both males and females send "visual signals" via their plumage. These signals are secondary sexual characteristics, sex-specific traits in males or females that are not directly involved in reproduction (Molles 2008). Bright colors and ornaments, such as large body size in male gorillas, antlers in moose, and bright colors in tails of male guppies, are all examples of secondary sex characteristics (Keyser and Hill 2000). Studies on guppies have shown that females prefer brightly-colored males. In guppies this choice is not merely aesthetic; rather, bright males sire more broods than unattractive males (Molles 2008).

The importance of secondary sexual characteristics of the eastern bluebird, *Sialia sialis*, has been studied extensively over the past decade. Eastern bluebirds range from Canada to Mexico and from the Atlantic Ocean to the Rocky Mountains, and are easily recognizable for the males' brilliant blue wings, back, and head, and orange chest (Figure 1; Gowaty and Plissner 1998). Bluebirds usually mate in monogamous pairs, with both parents taking time to watch over and feed the young (Siefferman and Hill 2003). They were once threatened by nest-site competition from invasive species such as European starlings and house sparrows, but conservation efforts of groups such as the American Bluebird Society have nursed the population back to health (Stokes and Stokes 1991, Gowaty and Plissner 1998). My family has aided the efforts by feeding birds in our backyard and putting up nestboxes that only bluebirds can access. As such, I have developed a fascination with the species, and have witnessed many bluebirds interacting and raising their young.

Figure 1. Male eastern bluebird (from Stokes & Stokes 1991)

As with the guppies mentioned above, the secondary sexual characteristic of plumage in bluebirds may be linked with individual quality and reproductive success. Several recent reports have examined the implications of color signals. I begin with a series of studies on male eastern bluebirds (Figure 1), testing the connection between plumage and male parental effort, competition for nesting sites, or offspring survival. I also investigated whether there is any evidence that plumage color affects female bluebird fitness (Figure 2). To determine whether the visual signals used by bluebirds are specific to this species or common to many songbird species, I compared the findings in bluebirds with studies of secondary sexual characteristics in three other songbird species.

CONNECTIONS BETWEEN PLUMAGE COLOR AND REPRODUCTIVE SUCCESS IN BLUEBIRDS

Songbirds are sexually dichromatic; female birds have plumage in the same color as the male, but it is duller (Gowaty and Plissner 1998; McGraw et al. 2004). Plumage—in bluebirds and other songbird species—reflects not only in the visible light range of humans, but the UV range as well. Studies have shown that eastern bluebirds are sexually dichromatic in both light ranges (Shawkey et al. 2005). Feathers have barbs that reflect light; these barbs are thicker in female bluebirds, therefore decreasing the amount of light that can pass through and causing them to appear dull in the visible range (Shawkey et al. 2005). In addition, male bluebirds have more melanin pigment than females in both their orange and blue plumage (McGraw et al. 2004), causing males to appear brighter. Plumage coloration of both sexes has been shown to influence mate choice, and potentially indicates the bird's reproductive quality (Shawkey et al. 2005).

Figure 2. Female eastern bluebird (from Stokes & Stokes 1991)

Between 1999 and 2005, Siefferman and Hill conducted a series of studies on plumage in eastern bluebirds. To test whether there was a relationship between color of male bluebirds and mate quality or reproductive advantage, they began a monitoring study in which they captured female and male bluebirds, tagged and then released them (Siefferman and Hill 2003). Over the breeding season they tested nestling weight and number of offspring per brood, and also observed male provisioning rate via video camera. They also collected feather samples from each adult bird for UV chroma and reflectance analysis. The study had several important results. First, males with more intense UV-blue coloration and larger orange breast patches paired with females that laid eggs earlier. Second, these same brighter males fed offspring more often and fledged heavier broods than dull males. Third, males with more UV color fledged a greater number of offspring. These results suggest that offspring of brighter males are in better physical condition and are more likely to survive (Siefferman and Hill 2003).

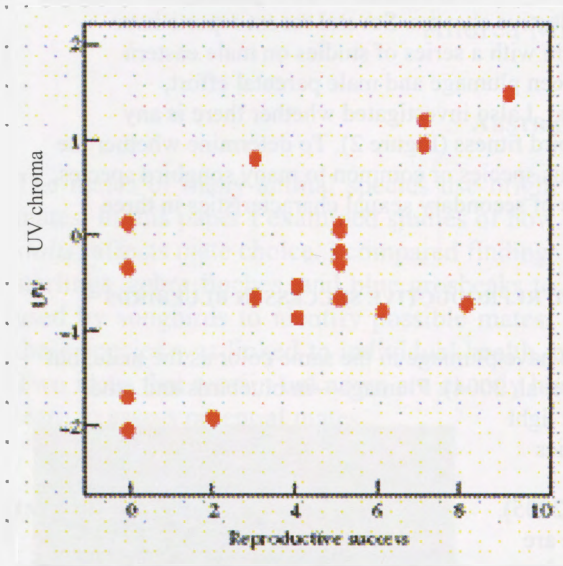

Figure 3. Relation of male UV chroma and reproductive success (number of offspring fledged) Log Scale.

Another aspect of reproductive success is success in establishing nest sites. Bluebirds nest only in secondary cavities (dead tree holes and holes made by other animals) or boxes, so the number of nesting spots available is always limited (Gowaty and Plissner 1998, Siefferman and Hill 2005a). Males without a nesting cavity cannot attract a mate. Siefferman and Hill (2005a) tested whether male plumage color was associated with success in competing for nest sites. Fifteen nestboxes were added to two study sites *without* previously-established bluebird populations, and then the areas were monitored for male-male fights, territory establishment, nest building, and date of first egg-laying. As in the previous study, males were banded and feathers were collected for analysis. They found that males with feathers that had high UV reflectance established nestboxes earlier than males with low reflectance; these same high-reflectance birds also had more body fat than their competitors (Siefferman and Hill 2005a). Both of these factors contributed to a brightly-plumaged male's ability to produce more offspring (Figure 3). Based on these results, Siefferman and Hill suggest that male coloration serves as a signal to potential competitor males (and males of other cavity-nesting bird species), but they did not directly test whether plumage color (or a related trait such as differences in energy or aggression) is the cue that determines the outcome of male-male competition.

Life history theory suggests that reproduction is energetically costly, and there must be tradeoffs between current reproductive effort and production of future ornamentation (Siefferman and Hill 2005b). To test whether there was a cost to males that had high parental effort, Siefferman and Hill (2005b) manipulated brood size and effect on male plumage the following season. Plumage was compared for males with reduced broods (2 nestlings) and males with enlarged broods (6 nestlings). Males with small broods invested little in caring for the nestlings, and as a consequence had very bright plumage in the following season. These bright second-year males then mated with better-quality females that laid eggs earlier. Males that had large broods in the first experimental year provisioned their offspring more often, then in the following year expressed duller coloration (Siefferman and Hill 2005b). Thus, males that began with only 2 nestlings likely "made up for" their lack of offspring by mating sooner and attracting better mates the subsequent year, while males that began with 6 nestlings invested more in caring for young and did not reproduce as well in the second season.

Age of males has also been shown to be correlated with plumage coloration (Siefferman and Hill 2003, 2005a). Age was estimated by the shape of primary feathers and the cycle of molt. The researchers found that both UV-blue coloration and body condition increased with age, and the largest difference was between yearling and two-year-old males (Siefferman et al. 2005). These studies show that plumage coloration can provide females with information on a male's age, health, and parental ability. In addition, males with brighter coloration and greater UV chroma fed incubating females more often (Figure 4) (Siefferman and Hill 2005c). Females that were better provisioned spent less time foraging, indicating that male bluebird plumage coloration has consequences not only for offspring fitness, but also benefits females.

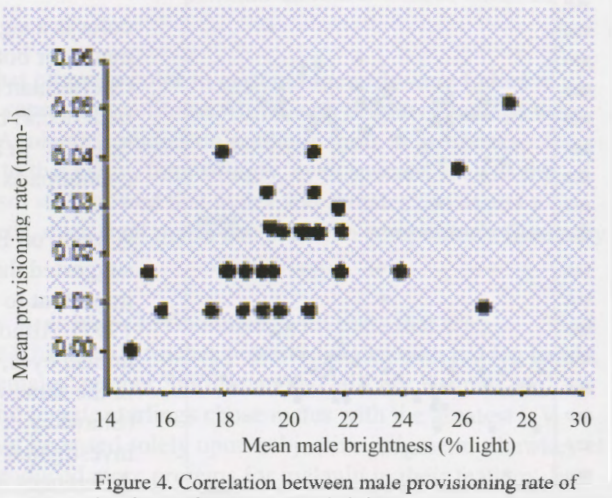

Figure 4. Correlation between male provisioning rate of incubating females and male brightness.

Although it is now clear that male plumage provides information on male quality, is it possible that female plumage also signals female quality? Female plumage is noticeably duller than that of the male due to less melanin pigmentation (McGraw et al. 2004), but significant color diversity is still observed in females (Shawkey et al. 2005). Siefferman and Hill (2005d) tested the effect of low food versus adequate food on plumage, body mass, and nestling provisioning behavior. Food-stressed females were duller, but did not have less body mass compared to control females. Also, females with brighter tail coloring, better body condition, and older females began to lay eggs earlier in the season; females with more colorful rumps and-better body condition provisioned offspring more often (Siefferman and Hill 2005d). It has also been shown that older females and those in better body condition are less susceptible to diseases and lay eggs with more pigmentation (Siefferman 2006). These data imply that female color can indicate female reproductive quality. Most importantly, in the same way females can assess male quality by coloration, males can also identify quality *females* by their color.

Comparison of Visual Cues and Mate Choice in Other Songbird Species

To assess whether visual cues are equally important in mate choice in other songbird species, I reviewed studies of secondary sexual characteristics in blue grosbeaks, European starlings, and zebra finches. Blue grosbeaks have strong color dimorphism between males and females (similar to bluebirds), zebra finches have moderate color dimorphism, and European starlings have the least color dimorphism between the sexes. Keyser and Hill (2000) tested whether plumage color was related to male quality in blue grosbeaks (*Guiraca caerulea*). They collected feathers, banded, and weighed the males, then kept records throughout a breeding season to observe color correlation with mass, physical condition, territory size/quality, and male feeding rate of nestlings per hour (Keyser and Hill 2000). They found that males with a higher blueness score had a larger body size than dull males (Figure 5). Second, two-thirds of the monitored males established breeding territories, and bluer males had larger territories. Third, although female grosbeaks fed offspring at a six-fold higher rate than males, the bluest males had the highest rate of feeding visits per hour (Keyser and Hill 2000). However, Keyser and Hill did not test whether plumage

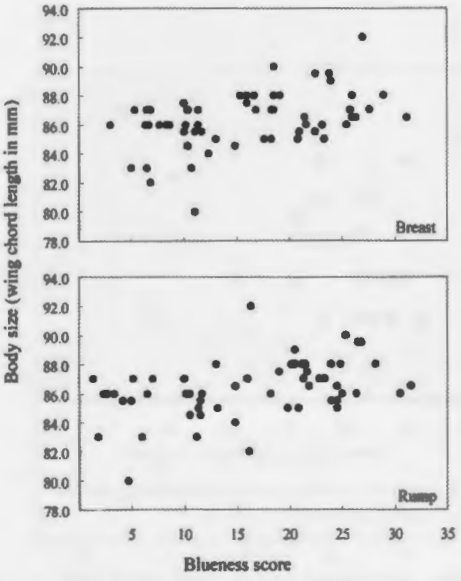

Figure 5. Correlation between male blueness and body size measured as wing chord length (mm).

color is a signal between rival males, potential mates, or both. Based upon bluebird studies (Siefferman and Hill 2005a-c) it is probable that both occur, but grosbeaks might react to plumage "signals" in a different way than their smaller counterparts.

A study on European starlings (*Sturnus vulgaris*) suggested that coloration signals are most important to females of the species (Bennett et al. 1997). Although starlings appear black and drab to human eyes, their feathers reflect in the UV range in the same way as bluebirds and grosbeaks (Shawkey et al. 2005). Bennett et al. (1997) investigated whether female starlings could detect differences in plumage coloration, based upon UV reflectance. Each female was allowed to visually assess four males, and her preference was measured as the length of time she spent with each male. In the first trial, no variables were manipulated, but in the second trial the same set of males were subject to a light that filtered out UV reflectance. They found that female starlings ranked males differently under the two treatments (Bennett et al. 1997), suggesting that both light environment and the amount of variation in UV reflectance is extremely important in mate choice decisions. Despite the minimal sexual dimorphism in plumage color (at least as apparent to humans), this study shows that female starlings do rank males based on differences in the UV reflectance of their plumage. More studies are needed to determine whether this plumage cue is correlated with health, siring ability, or parental behavior as in the bluebirds.

A study by Burley (1986) showed that mate choice was linked to reproductive success in zebra finches in ways similar to the bluebirds. Zebra finches (*Poephila guttata*), like bluebirds, are socially monogamous with both parents feeding the young. Instead of assessing plumage, Burley put different colored leg bands on each bird to test the role of visual cues in mate choice. Males were randomly banded with orange, red, or green, while females were not color-banded (The selected aesthetically-pleasing colors were known from previous experiments on finches.) Burley found that, out of 20 females, 11 mated to red-banded males, 4 to green-banded males, and 5 to orange-banded males. "Red" males mated with females that laid more eggs per clutch, and produced twice as many offspring as the other colors (Burley 1986).

In a second trial, Burley randomly banded females with blue, black, or orange bands and left males unbanded. As in the banded-male experiment, colors were determined from previous finch studies. Burley found that black-banded females produced an average of 18 offspring, while orange-banded females produced 12 and blue-banded 8 offspring. "Black" females also had the highest offspring survival rate (Burley 1986). Clearly female finches deemed red-banded males the most attractive (with the best potential reproductive benefit), and male finches deemed black-banded females the most attractive. As a result, the sexually-selected "preferable" colors did produce offspring with the best fitness. Even though the aesthetic trait was human-manipulated rather than natural as in the bluebird, grosbeak, and starling studies, it shows that birds of both sexes will select for certain traits more than others, and their discerning judgment is usually rewarded.

SUMMARY

Studies by Siefferman and Hill found that plumage color in eastern bluebirds were linked in multiple ways to individual quality and reproductive fitness. Birds with brighter plumage were healthier and sired healthier offspring. Analogous studies on aesthetic traits in grosbeaks, starlings, and zebra finches add weight to this claim. Interestingly, even species, such as the starling, that have less sexual dimorphism still showed that males and females can assess a potential mate via their color. In bluebirds, even rival males can predict a competitor's fitness by his plumage.

However, it remains to be seen *just how* birds know to find mates with traits that are advantageous. Burley did not determine why female finches preferred males with red leg bands, or why males preferred black-banded females; neither Siefferman and Hill nor Bennett et al. (1997) showed how female bluebirds and female starlings chose males with the greatest UV reflectance. Certainly mate choice cannot be based solely upon subjective judgment. Shawkey et al. (2005) showed that healthier birds produced more proteins for melanin in their feathers, but how do potential mates know to look for this quality? Selectiveness may be instinctive or learned. If the behavior is learned, do younger female bluebirds have less reproductive success than older females? To my knowledge this has not yet been studied. Perhaps future researchers also need to conduct studies linking duration or strength of a male bird's mating calls with plumage quality and reproductive fitness. Or perhaps there are traits such as pheromones or other chemical cues that have not yet been tested in birds. Determining how mate choice preferences evolve and the extent to which these preferences are learned or instinctive seems to be the next challenge.

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