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ORIGINAL ARTICLE

An experimental test of female choice relative to male structural coloration in eastern bluebirds

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Abstract Several experimental studies have shown that female birds use ornamental melanin and carotenoid plumage coloration as criteria in mate choice. Whether females choose mates based on natural variation in structural coloration, however, has not been well established. Male eastern bluebirds (*Sialia sialis*) display brilliant ultraviolet (UV)-blue plumage coloration on their head, back, wings, and tail, which is positively correlated with condition, reproductive effort, and reproductive success. We experimentally tested the hypothesis that female eastern bluebirds prefer as mates males that display brighter structural coloration by presenting breeding-condition females with males of variable coloration. We conducted two types of mate-choice experiments. First, females chose between males whose coloration was manipulated within the natural range of variation in the population; feathers were either brightened with violet marker or dulled with black marker. Second, females chose between males with naturally dull or bright plumage coloration. In both manipulated and unmanipulated coloration trials, female choice did not differ significantly from random with respect to structural coloration. We found no support for the hypothesis that the UV–blue coloration of male eastern bluebirds functions as a criterion in female mate choice.

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Introduction

Darwin (1871) first proposed that the bright ornamental coloration displayed by males of many animal species evolved in response to female mate preferences for brightly colored males. The hypothesis that females prefer as mates males with the most elaborate expression of color displays has now been experimentally tested in several species of passerine birds relative to expression of both the color quality of red and yellow carotenoid plumage coloration and the size of black eumelanin feather patches (Hill 2006). For both types of color display, convincing evidence has been published for female choice for extreme expression of color display within the natural bounds of color expression (summarized in Hill 2006).

Mate choice relative to expression of structural plumage coloration has received much less study than mate choice for pigment-based coloration. Variation in noniridescent, structurally based coloration results from coherent scattering of light from the spongy layer of feather barbs (Shawkey et al. 2003; Prum 2006), and this type of microstructure is often responsible for green, blue, and violet coloration. Most structural plumage coloration also has a substantial reflection in the ultraviolet (UV) region of the spectrum. By definition, UV light is invisible to humans, but it is part of the perceptual color space of diurnal birds (Cuthill 2006). UV coloration, therefore, must be taken into account in studies of the function of structural coloration (Bennett et al. 1997).

Most mate-choice studies that involve structural feather coloration have been conducted by removing UV reflectance. These studies eliminated UV reflectance by either

placing males behind UV-blocking windows (Maier 1993; Bennett et al. 1996; Hunt et al. 1997, 1999) or by applying UV-blocking chemicals to plumage (Andersson and Amundsen 1997; Siitari and Huhta 2002). In all studies, females discriminated against males that appeared to lack UV reflectance. These studies show that females see the UV component of feather coloration and avoid odd-looking males with no UV component to their plumage, but they do not test for preferences relative to natural variation in structural plumage coloration (Hill 2006).

In contrast to extensive literature on female choice relative to pigment-based coloration, only four experimental studies of female mate choice relative to natural variation in structural plumage coloration have been conducted. Bennett et al. (1997) tested female preference relative to natural variation in the iridescent structural coloration of males of European starling (*Sturnus vulgaris*) and found that females showed an association preference for males that exhibited coloration with greater reflectance in violet and red regions. Likewise, female blue tits (*Parus caeruleus*) prefer males with brighter non-iridescent UV–blue structural plumage (Hunt et al. 1998). Only two studies have manipulated structural coloration within natural variation to date. Ballentine and Hill (2003) manipulated the plumage of male blue grosbeaks (*Passerina caerulea*) to move them to the extremes of color expression in the wild population and found that the patterns of female choice relative to male color display did not differ significantly from random. By manipulating UV reflectance of male blue tits (*P. caeruleus*), Johnsen et al. (2005) found that females adjust parental effort in response to male appearance.

Manipulation of structural coloration within a natural range of expression represented an improvement over previous studies that used UV-blocking techniques in two important ways. First, such an experiment assesses female response to male coloration within a range of color displays that would occur among males in nature and thus places the mate-choice experiment with a relevant context. Second, by manipulating male coloration, the researcher is able to randomize plumage coloration with respect to all potential confounding variables (e.g. song, behavior, health, and vigor) and in this way conduct a more convincing test of the focal trait.

We tested whether female eastern bluebirds (*Sialia sialis*) use expression of UV–blue structural coloration of males as a criterion of mate choice. Eastern bluebirds are socially monogamous and sexually dimorphic passerines that breed throughout eastern North America (Gowaty and Plissner 1998). Males display conspicuous UV–blue structural coloration on their head, back, rump, tail, and wings. The coloration has a spectral reflectance peak that corresponds to approximately 400 nm and reflects UV and blue wavelengths of light equally (Siefferman and Hill 2003). Field studies show that males with brighter structural coloration gain a reproductive advantage. A field correlation study demonstrates that more colorful males paired earlier in the season and experienced greater reproductive success than less colorful males (Siefferman and Hill 2003). Field experiments indicate that more colorful males are better able to gain access to limited nesting resources (Siefferman and Hill 2005b). These patterns could result from brighter males either being more attractive to females during mate choice or gaining an advantage in competition with other males for resources.

The goal of this study was to test whether UV–blue coloration of males serves as an important criterion in female mate choice. We conducted our experiments in an aviary so that we could control male–male interactions and manipulate the coloration of males. We tested female choice for male coloration in two experiments. First, we manipulated the plumage coloration of stimulus males within the natural range of variation in the population to investigate whether females preferred brighter males. Second, we presented females with males with naturally bright or drab structural coloration. Because prior fieldwork showed that males that displayed brighter structural coloration paired earlier, we predicted that in both manipulated and unmanipulated plumage coloration trials, females would prefer brighter males.

Materials and methods

During the spring of 2002 and 2004, we used mist nets to capture adult eastern bluebirds from three different locations in Macon and Lee Counties, AL, USA. All birds were in adult breeding plumage but were of unknown age. We housed birds in unisex flocks of 5–8 birds per cage (2.5× 1.5×5 m) at an aviary in the campus of Auburn University. Before and during the experiment, captive birds were provided with water and a diet of meal worms (*Tenebrio molitor*), crickets (*Acheta domesticus*), and wax worms (*Galleria mellonella*) ad libitum.

Plumage measurements

We collected eight feathers from the rump of each male and taped the feathers on a black paper (Canson® Cat: #425 Stygian black) overlapping to recreate a colored patch. We measured the plumage reflectance using an Ocean Optics S2000 spectrometer and deuterium tungsten halogen light source (range 250–880 nm; Dunedin, FL, USA). All measurements were taken perpendicular to the feather surface using a metal fiber-optic probe mount with a rubber cap to exclude ambient light. We set the distance between the probe and feather at 5 mm to create a 2-mm measurement area. We generated reflectance data relative to a white standard (Labsphere®) using the OOIBase

software (Ocean Optics®). We took five measurements from each feather sample and averaged them to represent the UV–blue coloration of each male.

We summarized reflectance data by calculating three standard descriptors of reflectance spectra: brightness, chroma, and hue. Mean brightness was calculated as the mean summed reflectance ($R_{300–700\ nm}$). UV chroma was calculated as the proportion of the total reflectance ($R_{300–700\ nm}$) that is in the UV part of the spectrum ($R_{300–400\ nm}$). Blue chroma was calculated as the proportion of the total reflectance ($R_{300–700\ nm}$) that is in the blue part of the spectrum ($R_{400–500\ nm}$). Hue was calculated as the wavelength at peak reflectance. These calculations taken from the same spectral curves are correlated in eastern bluebirds (Siefferman et al. 2005) such that the most ornamented males display brighter coloration and greater UV chroma. Because past experiments have demonstrated that brightness of structural coloration but not chroma or hue is condition dependent (Siefferman and Hill 2005a), we chose to manipulate the brightness of male plumage coloration. Because we only took spectral measurements of each manipulated bird in 2004, some analyses only include the 2004 dataset.

General mate-choice methods

To be certain that the females did not choose between males with whom they might have had prior experience, we conducted each trial with males and females that were captured at different study areas. We conducted mate-choice trials in two large outdoor mate-choice arenas (6×8×2 m; Fig. 1) under natural light conditions. At the beginning of each mate-choice trial, we placed two males in adjacent cages that were separated by plywood. We placed a female in a third compartment that spanned the entire length of the aviary and allowed her visual and acoustic but no physical contact with the males. To facilitate natural breeding conditions and mate choice, we placed nest boxes between the female cage and both male compartments. The nest boxes were designed with two entrances so that males

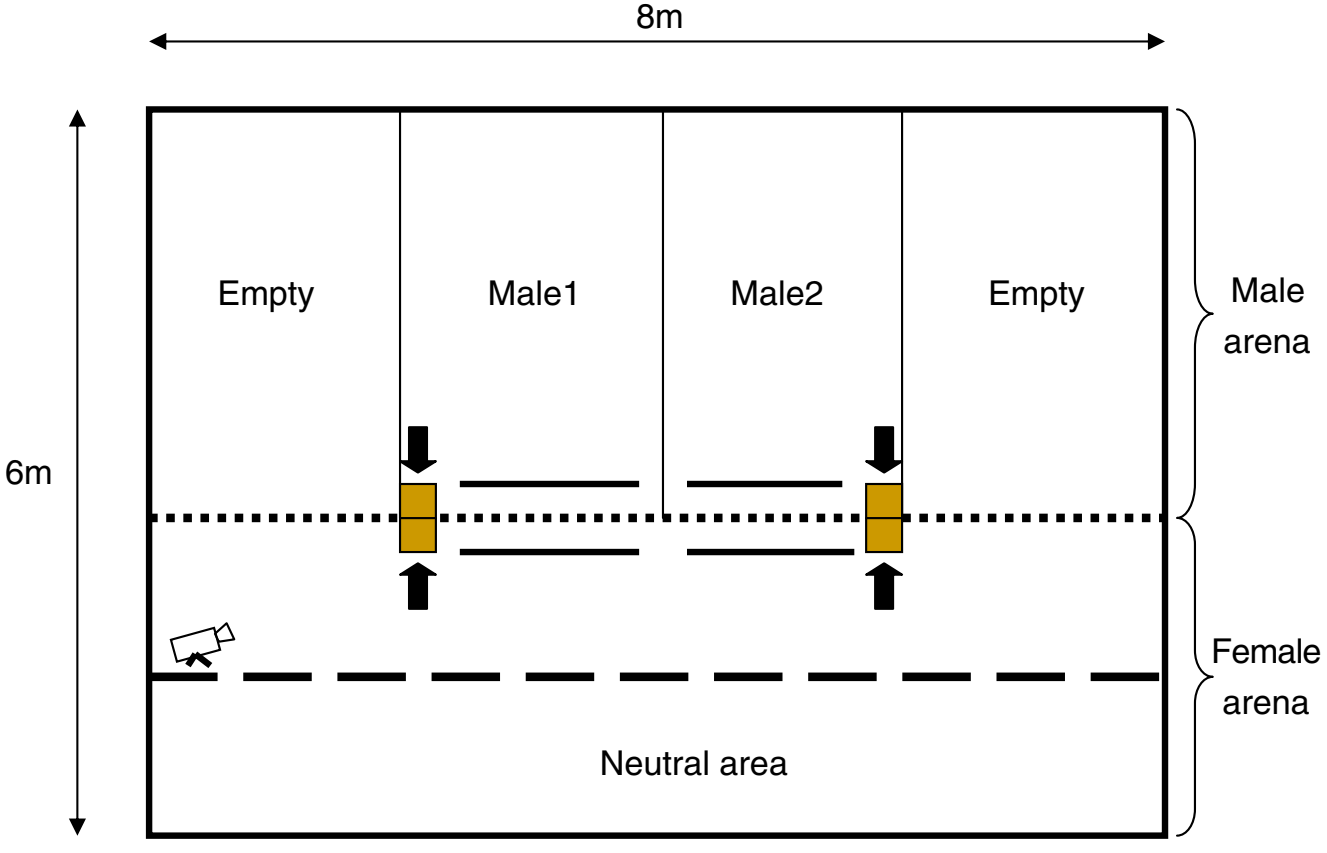

Fig. 1 Diagram of the outdoor mate-choice aviary used for the eastern bluebird female-choice experiment. The sexes are separated by central wall (*dotted line*) made of plywood on the bottom half and wire mesh on the top half; separations between male cages (*thin solid lines*) are plywood. Outer walls (*thick solid lines*) are plywood. The roof is made of wire mesh to allow natural light. The female area is separated by a long half-wall (ceiling to 1 m from floor, *long broken line*) made of plywood to allow the females in a "neutral area" that contained perches, food, and water and visually separated them from the males. For a female to display mate choice, she had to fly underneath the wall where she could view and interact with the males in two cages. Nest boxes with double entrances (*arrows point to entrances*) were mounted directly below each display perch. "Display perches" (*solid line*) are near the nest boxes, and when a female sat on these perches, we counted her as having visited the male in that cage

and females could enter the box freely, but birds were separated in the box by a mesh barrier (Saetre et al. 1994). All cages had many perches, and we positioned two "display perches" for the female directly in front of each male cage, approximately 0.2 m from the male cage. We used these "display perches" to calculate association time (Fig. 1). Females were allowed to choose between two simultaneously displaying males. Females also had access to a neutral area from which they had no visual contact with either male. Immediately after we placed the birds into the mate-choice arena, we videotaped (Sony Hi-8) the behavior of all three birds for three continuous hours. In nearly all trials, within 15 min of the commencement of the trials, males began to sing and display from the perches. After each trial, the birds were released to their original capture location, and several birds bred successfully later in the season.

In 2002 and 2004, we manipulated plumage coloration of males for mate-choice trials by enhancing or reducing plumage coloration. Males were assigned to treatment groups by pairing males of similar body size and natural plumage coloration and then randomly assigning males to treatment groups. We used nontoxic, black permanent marker (Sharpie® permanent marker: black) to decrease brightness of UV–blue color and violet permanent marker (PRISMACOLOR® PM-60: violet mist) to enhance brightness of UV–blue color. Note that because coloration of male bluebirds results from microstructure and not pigments, feathers colored with a black marker still looked blue to a human observer, and the reflectance from such feathers still had a spectral shape characteristic of blue (Fig. 2). The black ink from the pen uniformly absorbed a percentage of light reaching the microstructures, uniformly reducing the brightness of coloration.

We colored all blue feathers on the head, neck back, rump, tail, and wings of each male carefully. Because the marker temporarily wetted the feathers and changed the brightness of feathers perceptibly, we were certain that we applied an even coloration across the feathered surface of the bird. The markers dried quickly and did not cause the birds to look abnormal to the human observer. Markers were applied 10 min before the commencement of each trial.

Ideally, in a mate-choice experiment, each experiment would be conducted with a different set of stimulus males to avoid any possibility of pseudoreplication creating or obscuring patterns. In our experiment in which we tested up to 46 females in each experiment, this would have required maintaining 96 males in captivity. It was not feasible, and we felt not ethical, to capture such a large number of males. As a compromise, we used 16 different males to generate 24 dyads of males in 2002 and 21 different males to generate 26 dyads of males in 2004. Males were randomly assigned to a color manipulation, and males in the two groups did not differ significantly in size or premanipulation plumage coloration (Table 1). Three criteria were used when choosing dyads of males for mate-choice trials. First, males must have been captured from a different field site than females. Second, males were assigned to dyads such that each dyad was represented by a unique pair of males. Finally, within this subset of available males, we chose males randomly from large flight cages. We used a unique female for each mate-choice trial within an experiment. In 2004, we used 16 of the same females for the natural coloration experiment and the manipulated coloration experiment.

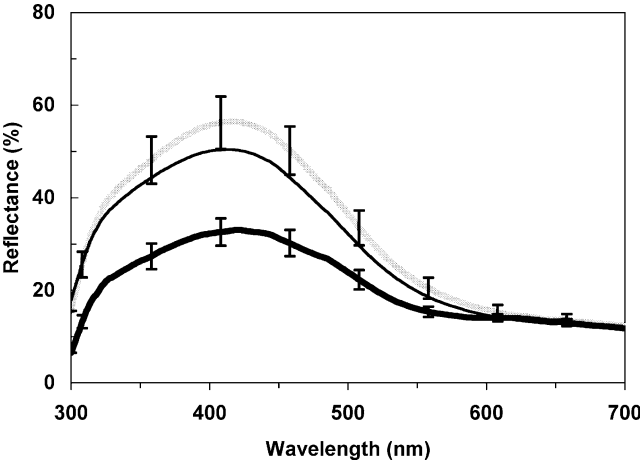

Fig. 2 Reflectance spectra of plumage coloration showing the effect of applying the enhancing marker and the reducing marker on the rump feathers of male eastern bluebirds. The *thick black line* is the spectrum after decreased treatment; the *thick gray line* represents the spectrum after the enhanced treatment, with SD error bars at every 50 nm interval. The *thin black line* represents the natural plumage color before marker treatment; error bars are excluded for clarity. *Note* We applied the same color treatment to every blue body region (all parts excluding breast and belly); the markers had a similar influence on all body regions

We also conducted mate-choice trials in which females were given the opportunity to choose between two males of natural plumage coloration. First, we measured plumage coloration, then we formed each trial by creating unique dyads by pairing males of similar body size that differed by at least 20% in brightness of their plumage. Early in the breeding season of 2004, we used 20 males to create 20 unique dyads of males and assigned a different female to each of the unique dyads.

Data analyses

We transcribed the video footage recorded for two continuous hours between 0.5 and 2.5 h after the commencement of trials. We began transcribing footage at 0.5 h after the commencement of the trials to allow

Table 1 Plumage coloration of male eastern bluebirds used in the 2004 mate-choice manipulation

	Decreased color (n=8)	Enhanced color (n=10)	t	P	Range of variation
Original brightness	28.35±1.83	31.44±1.63	1.26	0.23	46.59–16.68
Treatment brightness	21.24±2.02	32.74±1.80	4.25	<0.001	40.46–12.79
Original UV chroma	33.40±0.70	34.70±0.62	1.39	0.18	42.55–24.39
Treatment UV chroma	28.73±0.72	33.53±0.64	5.00	<0.001	35.30–24.49
Original blue chroma	40.61±0.34	40.56±0.30	−0.10	0.92	43.41–34.91
Treatment blue chroma	38.88±0.32	41.71±0.29	6.56	<0.001	42.97–37.56
Original hue (nm)	412.85±3.19	415.06±2.85	0.52	0.61	446.67–370.80
Treatment hue (nm)	424.00±3.03	417.30±2.71	−1.65	0.12	436.80–409.00
Wing chord (mm)	98.22±0.61*	98.78±0.61*	0.64	0.53	
Mass (g)	26.88±0.56*	27.93±0.56*	1.34	0.20	

Plumage data were not available for 2002 males. Data include coloration both before and after plumage manipulation as well as body size. Measures were compared using independent t tests. Pretreatment males were similar in plumage coloration and body size. Natural ranges of original color variables were based on a larger subset of 224 breeding males captured during 2003–2006.
*n=9

the birds to acclimate to their surroundings. Females had the opportunity to perch directly in front of males on the "display perches" or on many other perches. We defined total association time as the total time that the female perched on either of the "display perches" during the 2-h trial. As our index of preference, we calculated the proportion of time that a female associated with each male. We considered a trial to be a successful choice if the female spent ≥60% of her association time with one male. We conducted all the analyses using JMP 4.0.1 (SAS Institute). We tested for normality using Shapiro–Wilk tests, using parametric tests when data were normally distributed and nonparametric tests when assumptions of normality were violated.

Results

Color manipulation

The permanent marker treatments effectively changed the plumage coloration of male eastern bluebirds (Table 1, Fig. 2). By comparing the treatment with natural coloration of males taken over the course of four breeding seasons, we found that the resulting plumage coloration was within the natural range of variation in the breeding population (Table 1). The plumage brightness of one male, however, was manipulated below the natural range of variation. Although, the following analyses were conducted while both including and excluding the trials in which this male was used; the test results were similar. In general, the manipulation affected the overall brightness but changed the shape of the spectral curve very little, and there was no significant effect on hue. Although the proportional UV and blue reflectance (chroma) were influenced by the manipulation (Table 1), this is mainly because the manipulations altered the reflectance between 300 and 600 nm without altering the reflectance in the longest wavelengths ($R_{600–700\ nm}$; see Fig. 2).

Mate-choice experiment: general responsiveness

Both male and female bluebirds interacted during trials in a manner that suggested that they were receptive to forming pairs and mating. During trials, males were active, usually sang typical songs and often made high-pitched "courtship" vocalizations, fanned their tails, and displayed their rumps to females. In turn, females interacted with males via vocalizations and inspection of nest boxes. Some females even began building nests.

Mate-choice experiment: manipulated plumage

We conducted 24 trials in 2002 and 26 trials in 2004; however, one female in 2002 and three females in 2004 did not make a clear choice of mate. We found no differences in the preferences for duller and brighter males according to year (χ^2=2.13, df=1, P= 0.14); therefore, we combined the data from 2002 and 2004. We found no evidence that females preferred brighter males; 23 females preferred males that exhibited increased plumage coloration, and 23 females preferred males that exhibited decreased plumage coloration (χ^2=0.00, df=1, P=1.00; Fig. 3a). A subset of females spent time in nest boxes. Again, we found no evidence that females preferred brighter males; 11 females that visited nest boxes preferred brighter males, and nine females that visited nest boxes preferred males that exhibited duller plumage coloration (χ^2=0.20, df=1, P=0.66). Three females initiated nest building in nest boxes. Again, we found no evidence that females preferred brighter males;

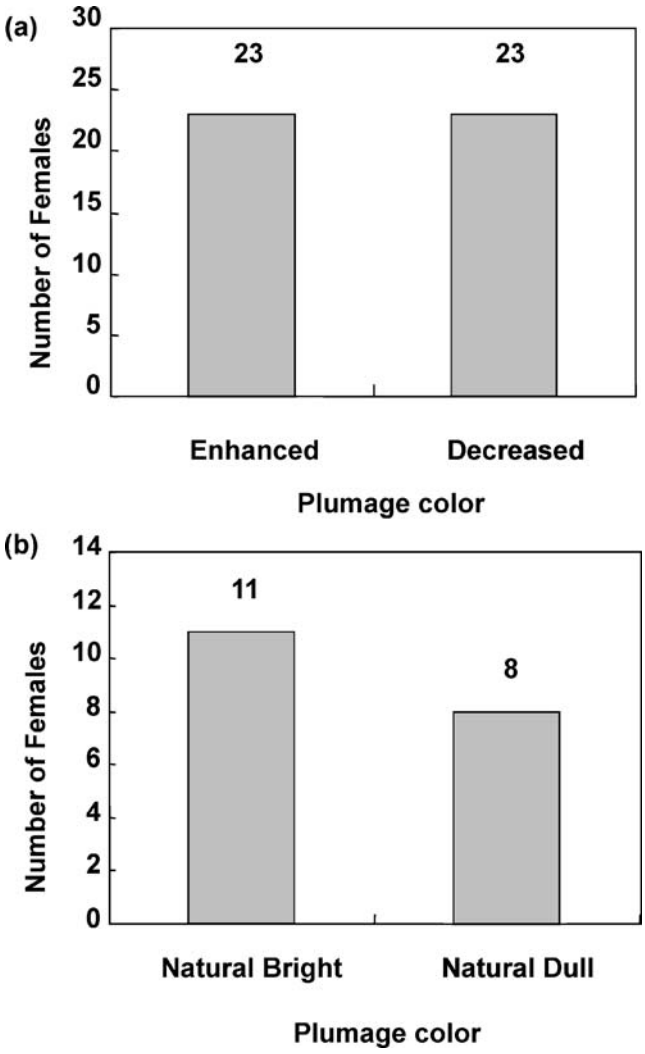

Fig. 3 Number of female eastern bluebirds that chose brighter or duller males in mate choice trials for **a** males displaying manipulated coloration and **b** males displaying unmanipulated coloration

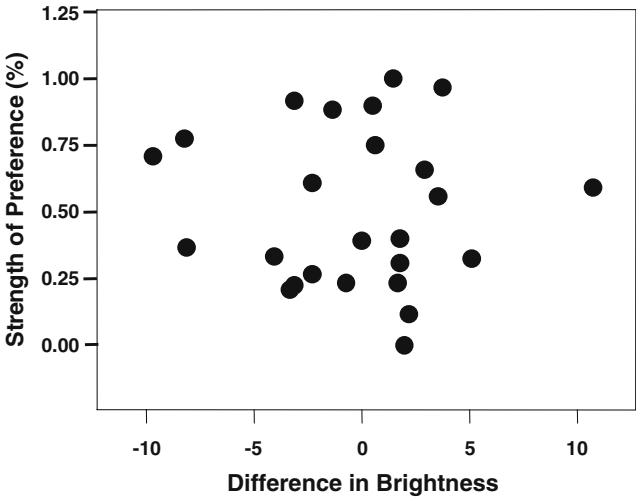

Fig. 4 Relationship between female association time and relative difference in plumage brightness of males in each dyad. A strength of preference of 1 represents a female that spent all her time with one male

one female that built a nest preferred brighter males, and two females that built nests preferred males that exhibited duller plumage coloration.

We used linear regression to determine whether the strength of the females' preference was influenced by the difference in color of two males in the dyads. We found no significant relationships between female association time and relative difference in plumage brightness ($R^2<0.01$, $F_{1,23}=0.03$, $P=0.86$; Fig. 4), UV chroma ($R^2<0.01$, $F_{1,23}<0.01$, $P=0.99$), blue chroma ($R^2<0.01$, $F_{1,23}=0.01$, $P=0.91$), or hue ($R^2<0.01$, $F_{1,23}<0.01$, $P=0.94$).

Mate-choice trials using natural coloration

We conducted 20 mate choice trials in which females chose between two males with unmanipulated plumage coloration. In one of these trials, a female did not spend ≥60% of their time with one male and thus, by our criteria, made no obvious mate-choice decision. Of the 19 trials in which females made definite mate-choice decisions, we found no evidence that females preferred brighter males; 11 females preferred males that exhibited brighter coloration and eight females preferred males that exhibited duller coloration ($\chi^2=0.49$, $df=1$, $P=0.47$; Fig. 3b). Moreover, we used paired t tests to compare the color characteristics of the winners and losers of each trial. Again, we found no significant difference in the plumage brightness ($t=0.20$, $n=19$, $P=0.84$), UV chroma ($t=-0.18$, $n=19$, $P=0.86$), blue chroma ($t=-1.14$, $n=19$, $P=0.27$), or hue ($t=0.07$, $n=19$, $P=0.94$) of males that were preferred and not preferred. Furthermore, because dyads varied in the degree of difference in coloration between the brighter and duller males, we used linear regression to investigate whether there were relationships between the strength of female preference and the difference in the plumage coloration of males. We found no significant relationships between female association time and relative difference in plumage brightness ($R^2=0.04$, $F_{1,18}=0.7$, $P=0.41$), UV chroma ($R^2<0.01$, $F_{1,18}=0.09$, $P=0.77$), blue chroma ($R^2=0.12$, $F_{1,18}=2.53$, $P=0.13$), or hue ($R^2=0.02$, $F_{1,18}=0.33$, $P=0.57$).

We calculated the power of our manipulated mate-choice experiment (Power=0.98, $n=46$) by using previous studies that found that ≥80% of females preferred more ornamented males. Lastly, by combining data from all of the mate-choice experiments ($n=65$), we tested whether females displayed a preference for one side of the mate-choice chamber. We found no differences in the preferences for males on the right or left side of the chamber ($\chi^2=1.86$, $df=1$, $P=0.17$).

Consistency of choice

Although each trial represented a unique trio of birds (one female and two males), in some cases, males were used more than one time, and 16 of the females that were used in the artificially manipulated coloration trials were also used in the natural coloration trials. We investigated whether individual males were consistently chosen by females. In the mate-choice experiment in which females were given the opportunity to choose between two males of manipulated plumage coloration, 13 of the 17 (76%) males were not consistently chosen or not chosen at all by females. In natural coloration trials, 10 of 14 (71%) males that were used in multiple trials were not consistently chosen or not chosen at all by females. Moreover, when males were used in more than one trial, we calculate a winning rate for each male (number of winning trials/total number of trials). We used linear regression to test whether the proportional winning rate was related to spectral measures of manipulated plumage coloration. The winning rate was not significantly related to the brightness, UV chroma, blue chroma, or hue of the structural coloration (all $P>0.1$). Sixteen females were used in both manipulated and natural plumage coloration trials. Females did not consistently choose either the brighter or duller male ($X^2=0.25$, $df=1$, $P=0.62$).

Discussion

We found no support for the hypothesis that female eastern bluebirds prefer to mate with males with more elaborate structural ornamental plumage coloration, regardless of whether we conducted trials with males whose plumage was manipulated or not manipulated. Females showed no preferences for males displaying brighter blue feathers or blue feathers with greater UV chroma, greater blue chroma, or more UV-shifted hues. These results were surprising because prior field correlations indicated that structural coloration of males is a sexually selected trait that reliably conveys information about male condition (Siefferman and Hill 2005a), age (Siefferman et al. 2005), and breeding success (Siefferman and Hill 2003). Negative results for mate choice are only convincing if experiments have sufficient power and if test animals are receptive to stimulus animals. Our sample size was relatively large for a mate-choice experiment, and we observed the same indifference to color display in two separate mate-choice experiments. Many experiments assessing choice of mates based on expression of carotenoid or eumelanin coloration and using an aviary design similar to what we used have found positive results with many fewer trials (Hill 1990; Sundberg 1995; Kimball 1996).

Our findings are also unlikely to simply be an effect of captivity. All of the females used in this experiment were in reproductive condition, and we are confident that females were actively choosing males. Behavioral observations during trials indicate that both males and females displayed courtship behaviors and that females often inspected nest boxes. Indeed, if association preference is considered a weak measure of mate preference, we can use box visitation, which is a much less ambiguous indicator of preference. For the subset of females that visited boxes, mate choice was random with respect to plumage coloration. We assert that our mate-choice trials represent convincing evidence that female bluebirds were not using variation in brightness or chroma of structural coloration to choose males. Our experiment, however, did not quantify or manipulate the melanin-based breast coloration of the eastern bluebird. It is possible that mate-choice decisions of females are influenced by the patch size or coloration of the orange breast plumage. Indeed, in the past research, using a composite color score including variation in both melanin and structural coloration, we found that males with larger, darker melanin patches and brighter UV–blue coloration fed chicks more often and were mated to females that began laying eggs earlier in the season (Siefferman and Hill 2003). Moreover, we did not measure or manipulate other variables, such as song and age that may also have influenced association preferences.

In addition to female choice, male–male competition, and a combination of male–male competition and female choice, can drive the evolution of ornamental traits in many species (Andersson 1994; Berglund et al. 1996). Environmental constraints often influence the evolution of male–male competition vs female preferences in animal mating systems (Reynolds 1996). For instance, when breeding sites are readily defensible, male–male competition is probably more important than female choice in influencing male reproductive success. Bluebirds are obligate secondary cavity nesters, and male and female bluebirds compete vigorously against same-sex conspecifics for nest sites (Gowaty and Wagner 1988). It may be that structural coloration in eastern bluebirds functions as a reliable indicator of male competitive ability and is used in mediating contests over nests' sites. Indeed, an experiment in which the settlement pattern of bluebirds was assessed relative to male plumage coloration indicated that male plumage coloration was a good predictor of male resource-holding potential (Siefferman and Hill 2005b).

In the field, we have observed relationships between the plumage coloration of male eastern bluebirds and the first egg date of females, paternal feeding rates, and offspring condition. These patterns could be used as indirect evidence that females use male coloration in choosing mates. Such patterns, however, are also consistent with structural

coloration serving as a signal primarily in male–male contests. If structural coloration functions in male–male competition for access to high-quality territories, brighter males may pair earlier, feed offspring more often, and experience greater reproductive success because insect abundance is higher in their territories. Perhaps females choose mates by assessing territory quality and not plumage coloration. Our studies of eastern bluebirds illustrate how very difficult it can be to tease apart the potential roles of male–male competition and female choice of male in the field and hence the value of controlled aviary mate-choice experiments.

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