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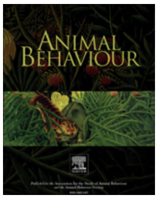

A field test of female mate preference for male plumage coloration in eastern bluebirds

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A growing body of evidence shows that female birds use male plumage coloration as an important criterion in mate choice. In the field, however, males with brighter coloration may both compete better for high-quality territories and be the object of female choice. Positive associations between territory quality, male–male competitive ability and female preferences can make it difficult to determine whether females actively choose the most ornamented males. Male eastern bluebirds, *Sialia sialis*, display brilliant ultraviolet (UV)-blue plumage coloration on their heads, backs, wings and tails and chestnut coloration on their breasts, which is positively correlated with condition, reproductive effort and reproductive success. We tested the hypothesis that female bluebirds prefer males that display brighter and more chromatic coloration by experimentally widowing males in the field and allowing replacement females to choose partners. We controlled for the influence of territory quality on female choice by widowing dyads of males with adjacent territories. We found no evidence that UV-blue or chestnut plumage coloration, body size or body condition predicted the male with which a female would pair. We found no support for the hypothesis that the coloration of male eastern bluebirds functions as a criterion in female mate choice.

It is generally thought that the bright plumage coloration displayed by males of many bird species evolved in response to selection from female choice for elaborate displays (Hill 2006). Indicator models of sexual selection propose that the expression of sexually selected traits, such as plumage coloration, reliably signal individual condition (Andersson 1994; Hill 2002). These traits can act as honest signals of an individual's phenotypic or genetic quality if only exceptionally fit individuals in a population achieve maximum expression of such traits (Zahavi 1975; Hamilton & Zuk 1982; Kodric-Brown & Brown 1984). Indicator models predict that individuals that display more exaggerated traits compete better for mates and thus experience higher reproductive success. There is now substantial experimental and correlational evidence that, in some species of birds, females discriminate between potential mates by assessing colourful plumages (reviewed in Hill 2006).

Studies of female mate choice in birds range from weak correlative field studies and uncontrolled aviary observations to carefully controlled experimental tests in both the field and the laboratory. Laboratory experiments can be useful because they allow researchers to manipulate coloration and disassociate colour traits from other correlated traits. Eliminating the confounding influence of male–male competition, for example, can be very helpful (Wagner 1998). However, eliminating male–male competitive interactions usually necessitates that males are housed individually and thus reduces physical access to females. When females do not have physical access to potential mates and cannot copulate with males, researchers generally use association time as a proxy for mate choice. Association time, however, may not always be an accurate and consistent measure of mate preference (Hill 2006). Females also may not make mate-choice decisions in the relatively unnatural environment of the laboratory. Finally, in laboratory-based mate-choice trials, it becomes difficult for researchers to investigate the fitness consequences of mating decisions (Hill 2006). For example, for most species in the laboratory, it is not possible to examine how the chosen male contributes to the female's breeding success. Contributions to reproductive success

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include direct benefits (territory quality and parental care) and indirect benefits (fertilization rate and genetic quality) provided by males. Controlled tests of female preferences conducted in the field provide an alternative to laboratory-based trials and can allow researchers to quantify both female choice and the ramifications of those choices.

The eastern bluebird, *Sialia sialis*, is among the better studied bird species with respect to the function of ornamental plumage coloration, and yet the importance of male coloration as a criterion in female mate choice remains uncertain. Male bluebirds display a structural UV-blue coloration on the plumage of their backs, heads, wings and tails and chestnut melanin coloration on their breasts compared with the overall duller coloration in females. Although no studies have examined visual perception in eastern bluebirds, UV vision has been shown in closely related species (Hart et al. 2000) and UV-blue coloration in passerine birds has been suggested to play an important role in signal communication (Hunt et al. 1999; Hill 2006). A correlative field study of eastern bluebirds shows that male eastern bluebirds with brighter UV-blue plumage and darker melanin breast colour pair earlier in the season, feed chicks more often, and gain higher reproductive success (Siefferman & Hill 2003). Experimental manipulations of paternal investment show that UV-blue structural coloration is a condition-dependent trait in bluebirds (Siefferman & Hill 2005a). Although the field correlative study linking coloration, earlier pairing and reproductive success suggests that females may use coloration to choose mates, experimental manipulations of structural coloration in an aviary show no consistent relationship between male UV-blue coloration and female association time (Liu et al. 2007).

Bluebirds are obligate cavity-nesting passerines and males that express more-ornamented UV-blue coloration are more successful competitors for limited nest sites (Siefferman & Hill 2005b). Thus, in the eastern bluebird as in many species that defend key resources necessary for reproduction, female choice for male coloration is confounded by female choice for the superior resources defended by brighter males. Simple correlative studies cannot distinguish the relative influences of female choice of mate and male–male competition in driving the elaboration of plumage coloration.

To test female preferences for ornamental plumage coloration more directly in a wild population of breeding eastern bluebirds, we conducted a mate-removal experiment. We removed the original mates from males to quantify the latency time for males to establish new pair bonds. We used this protocol to avoid any bias associated with prior pair bonds, because past relationships can confound mate choice in two ways. Pairs that have previous breeding experience in the same territory might experience advantages in acquiring nesting sites (Qvarnstrom & Forsgren 1998) and in reproductive success (Ligon 1999). We removed the mates of two males that held neighbouring territories with the assumption that males with adjacent territories held territories of similar quality. This experiment was designed to measure female preference in the wild and to quantify the breeding success of the subsequent mate selection on a platform of equal-quality territories.

First, by removing the original mates early in the breeding season, we caused pairs to reconstruct the early breeding season processes of mate choice and pairing. Territories from which females had been removed represented available males. Second, we investigated the characteristics of the males and determined which traits predicted male attractiveness to females. We tested the hypothesis that female eastern bluebirds prefer to pair with males that display the more-ornamented plumage coloration. Additionally, by monitoring the behaviour of the newly formed pairs throughout the breeding season, we quantified reproductive success.

METHODS

General Methods

Breeding cavities are probably the key resource that limits reproduction in eastern bluebirds (Gowaty & Plissner 1998). Nonbreeding birds (floaters) are present in suitable habitats, are sexually mature and display breeding condition (M. Liu, personal observation). When breeding opportunities become available (the original box owners die or disappear from a territory), these floaters frequently assume the territory and breed with widowed birds.

This study was conducted from March to August of 2005 and 2006 in two field sites, located in southeastern Alabama, U.S.A., with a total of 200 nestboxes. The distance between nestboxes was approximately 100 m. The habitat consisted mainly of pastures and hay fields surrounded by fragmented pine forests.

In this long-term research population, the birds were captured and banded in the early breeding season (1–15 March), before the experiment began. At each field site, we also monitored all other unmanipulated territories. To capture birds, we lured pairs into mist nets by playing recordings of eastern bluebird calls. Each bird was individually marked with a unique combination of three coloured bands and one U.S. Fish and Wildlife Service aluminium band. We measured body mass (accuracy 0.1 g) and the length of tarsi, wings and tails (accuracy 0.5 mm). We used principle component (PC) analysis to reduce our morphological measurements (tarsus, wing, tail) into PC scores. Principal component 1 explained 62.5% of the variation in morphological measurements. Body condition was calculated as the residuals of a regression of body mass on PC1 of body size (Jakob et al. 1996).

At the time of capture, we carefully plucked 8–10 rump (blue) and breast (chestnut) feathers. Feathers were placed in envelopes and stored in a temperature- and humidity-controlled laboratory before analysis. We taped feathers onto black paper (Canson cat. no. 425 Stygian black) using an overlapping fashion to mimic how feathers naturally occur on the birds. We measured the plumage reflectance using an Ocean Optics S2000 spectrometer and deuterium–tungsten halogen light source (range 250–880 nm). We used a fibre-optic cord equipped with a black rubber cap on the metal probe to exclude ambient light. The distance between the probe and the feather was set to 5 mm to create a measurement diameter of approximately 2 mm. The probe was perpendicular to the feather surface. We took all colour measurements at the same setting and the same person (M. L.) processed all data. We generated reflectance data relative to a white standard (Labsphere, Inc.) using OOIBase software (Ocean Optics). We measured each feather sample five times and used the mean to generate colour scores for each male.

For chestnut coloration (Fig. 1), we summarized reflectance data by calculating two standard descriptors of reflectance spectra: brightness and chroma. Mean brightness was calculated as the mean summed reflectance ($R_{300\text{–}700\text{nm}}$). Red chroma was calculated as the proportion of the total reflectance ($R_{300\text{–}700\text{nm}}$) in the red part of the spectrum ($R_{575\text{–}700\text{nm}}$). For UV-blue colour (Fig. 1), we calculated three standard descriptors of reflectance spectra: brightness, chroma and hue. Mean brightness was calculated as $R_{300\text{–}700\text{nm}}$. UV chroma was calculated as the proportion of $R_{300\text{–}700\text{nm}}$ in the UV part of the spectrum ($R_{300\text{–}400\text{nm}}$). Blue chroma was calculated as the proportion of $R_{300\text{–}700\text{nm}}$ in the blue part of the spectrum ($R_{400\text{–}512\text{nm}}$). Hue was calculated as the wavelength at peak reflectance. Calculations taken from the same spectral curves are correlated in eastern bluebirds such that the most ornamented UV-blue males display brighter coloration, greater UV chroma, and hues with wavelengths shifted towards the shorter wavelengths