



UV-blue structural coloration and competition for nestboxes in male eastern bluebirds

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Recent studies suggest that structural plumage coloration can indicate male quality and is used in female mate choice decisions. Whether or not structural coloration functions as a signal in male–male competitive interactions, however, has not been studied. Male eastern bluebirds, *Sialia sialis*, have brilliant ultraviolet-blue plumage on the head, back, wings and tail that is correlated with both reproductive effort and reproductive success. Bluebirds cannot excavate their own nest cavities, and as a consequence of limited nest sites, often engage in intense competition for nestboxes. We experimentally tested the hypothesis that structural coloration reflects male competitive ability by manipulating the number of available nestboxes. We erected a limited number of nestboxes in early spring and, after birds has established residency in those nestboxes, we added more nestboxes to the study site. We found that the reflective properties of the ultraviolet-blue plumage differed between males that acquired nestboxes early versus late in the spring, indicating that more colourful birds won competitions for access to nest sites. We also found that more colourful males fledged more offspring. These observations support the hypothesis that structural plumage colour is a condition-dependent trait in male eastern bluebirds that could be used to accurately assess the fighting ability of competitors.

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A common avian mating system involves resource defence whereby males compete for nesting sites that are necessary for attracting females (Ligon 1999). For birds that nest in secondary cavities, nest sites are often a key limiting resource, so a male's competitive ability should directly affect his reproductive success. Frequent contests with unfamiliar individuals favour the evolution of traits, such as colourful plumages, that honestly and reliably communicate male fighting ability or dominance (Pärt & Qvarnström 1997; Senar 1999). Sexual selection theory proposes that ornamental traits can reliably signal individual quality if the traits are condition dependent, such that only exceptionally fit individuals in a population achieve the maximum expression (Zahavi 1975; Kodric-Brown & Brown 1984; Grafen 1992). If the outcome of a costly fight is predictable, both contestants will benefit from signalling fighting ability (Rohwer 1977; Rohwer & Ewald 1982). For example, traits that were classically thought to be weapons, such as the antlers of ungulates, may also function as signals revealing the fighting ability of males and thus serve to settle contests without

dangerous and costly fights (Barrette & Vandal 1990; Berglund et al. 1996).

Colourful plumage in birds has long been thought to evolve to serve specific signal functions (Darwin 1871). Ornamental plumage coloration results primarily from either pigments deposited in feathers or feather microstructure. Pigment-based bird plumages are the best studied class of feather coloration and have been shown in many species to play an important role in conspecific interactions (Andersson 1994; Hill 2002). The signalling function of structurally based plumage coloration, in contrast, is not as well studied. Structural coloration is produced by the microstructure of the medullary layer of feathers. This microstructure coherently scatters wavelengths of light giving feathers green, blue, purple, ultraviolet or iridescent coloration (Dyck 1971a, b; Prum et al. 1999a, b). The colour display produced by feather microstructure usually includes portions of the ultraviolet (UV) range of the electromagnetic spectrum, so much of the variation in this type of plumage coloration is imperceptible to human researchers (Bennett et al. 1994). The visual system of most bird species, including all passerine birds tested to date, however, is sensitive to UV wavelengths (Cuthill et al. 2000).

Female mate choice for males with greater UV reflectance appears to drive selection for structural plumage

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traits in some species (*Luscinia svecica*: Andersson & Amundsen 1997; Johnsen et al. 1998; *Sturnus vulgaris*: Bennett et al. 1997; *Parus caeruleus*: Andersson et al. 1998; Hunt et al. 1998; Sheldon et al. 1999; Delhey et al. 2003; *Ficedula hypoleuca*: Siitari et al. 2002). Moreover, studies have shown that structural plumage colour can reliably signal territory quality (*Guiraca caerulea*: Keyser & Hill 2000), reproductive effort (*Sialia sialis*: Siefferman & Hill 2003), parasite load (*Ptilonorhynchus violaceus*: Doucet & Montgomerie 2003) and viability (*Parus caeruleus*: Sheldon et al. 1999). These studies provide evidence that structural plumage coloration can indicate mate quality of males. Whether or not structural coloration also functions as a signal of fighting ability in male–male competitive interactions remains virtually unstudied.

Eastern bluebirds, *Sialia sialis*, are a particularly appropriate study species to investigate the relation between structural plumage ornamentation and male competitive ability because males have brilliant UV-blue structural plumage and compete vigorously for nest sites. Because bluebirds cannot excavate their own nest cavities, and natural cavities are limited in the environment, there is intense competition between male bluebirds (and other cavity nesting birds) for nestboxes (Hersey 1933; Gowaty 1981). Eastern bluebirds are socially monogamous songbirds that have sexually dichromatic plumage; males have bright UV-blue on the back, head, wings and tail, and chestnut on the breast, whereas females are duller with greyish-blue on the head, back, wings and tail, and duller chestnut breasts. In Alabama, eastern bluebirds breed from late March to August and often produce three successful broods in a season. In a recent study, we demonstrated that the UV-blue of male eastern bluebirds is related to timing of breeding, male reproductive effort and reproductive success (Siefferman & Hill 2003). Here, we conducted an experiment to test whether structural plumage coloration in eastern bluebirds can indicate male competitive ability by studying the relation between plumage coloration and body fat, body condition and access to limited nest sites.

METHODS

This study was conducted from March to May 1999 in Lee County and March to May 2001 in Macon County, Alabama. Each 5-km² study site consisted of pastures and hay fields interspersed with fragments of young pine stands. Before the experiment, both study sites contained suitable bluebird habitat but virtually no nest sites. We purposefully chose field sites without established bluebird populations because individuals with a prior history of interaction might rely less on signalling during agonistic interactions (Lemel & Wallin 1993) and because the outcomes of territorial disputes may be affected by previous nest site knowledge and order of occupancy (Qvarnström & Forsgren 1998).

At each study site, we added 15 nestboxes during two stages: (1) during initial territory settlement before any nests were built in the population ('early'; 10–15 March); and (2) after many males had established territories and

many females had initiated nesting ('late'; 15–20 April). Early nestboxes were placed at least 200 m apart and late nestboxes were interspersed between them. We monitored each nestbox at least once every 3 days to record male–male contests, male territory establishment, nest initiation and first egg dates. At the Lee County site in 1999, we monitored all subsequent nesting attempts and quantified the total number of offspring fledged.

We only included a male in our tallies of successful box owners if his mate had initiated laying before 1 May because, after this date, new pairs could have moved to the field site following a failed nesting attempt elsewhere earlier in the season. Our estimate of re-nesting timing is based on 5 years of monitoring a population of eastern bluebirds in Alabama and our observation that individuals that experience nest failure early in the season do not initiate re-nesting before 10 May. We captured males with mist nets during incubation and with traps while they fed chicks. Each bird was individually marked with a unique combination of colour leg bands and a U.S. Fish and Wildlife Service aluminium leg band. We measured mass to the nearest 0.5 g, tarsus to the nearest 0.01 mm, and scored fat of the furculum and abdomen on a five-point scale (Helms & Drury 1960). We estimated age as either second-year or after-second-year using the characteristics of the 10th primary feather (Pitts 1985). We used the ratio of mass to tarsus as an index of condition.

At time of capture, feather samples were collected from 35 adult males for spectrophotometric plumage analysis. From each bird, we carefully plucked nine rump and the two outer tail feathers. The feathers were placed on black paper such that the rump feathers overlapped in a fashion that mimicked the way the feathers naturally lay on the bird. One researcher (L.S.) recorded spectral data with an Ocean Optics S2000 spectrometer (range 250–880 nm: Dunedin, Florida, U.S.A.) using a micron fibre-optic probe at a 90° angle to the feather surface (see detailed methods in Siefferman & Hill 2003). To smooth the curve, each reading was constructed from an average of 20 reflectance curves. We took five readings from each region, moving the probe by at least 3 mm before taking each new reading. Finally, we averaged the readings from both the rump and the right and left tail feathers of each male.

We summarized reflectance data by calculating three standard descriptors of reflectance spectra: brightness, UV chroma and hue. Brightness, or the total amount of light reflected by the feather, was calculated as the mean of the summed reflectance from 300 to 700 nm. UV chroma, a measure of spectral purity, was calculated as the ratio of the total reflectance in the ultraviolet range to the total reflectance of the entire spectrum ($\int_{300-400} / \int_{300-700}$). Hue, the principal colour reflected by the feather, was calculated as the wavelength (nm) corresponding to maximal reflectance (λ_{max}).

Statistical Analyses

Our data became normally distributed after calculating a log transformation on brightness, hue and the tarsus-to-mass ratio and an arcsine transformation on UV

chroma (proportional data). We found significant variation due to year and settlement site on plumage colour, body condition and fat content (t test: $P_s < 0.01$); therefore, we standardized the data for each year to a mean of zero and a standard deviation of one. We used a backward stepwise logistic regression to determine whether measures of plumage colour and measures of individual condition predicted settlement speed. We used a Fisher's exact test to determine whether age predicted settlement patterns. We used two-tailed correlations to determine whether measures of plumage colour were related to time of capture and reproductive success. Values are given as means \pm SD. We performed statistics using SPSS 11.5 (SPSS 2002).

RESULTS

In 1999, nine males acquired early nestboxes and 10 males acquired late nestboxes. In 2001, eight males acquired early nestboxes and eight males acquired late nestboxes. We used a backward stepwise logistic regression to determine whether brightness, UV chroma, hue, body condition or fat content predicted settlement speed. UV chroma, body condition and fat contributed significantly to the model that predicted settlement speed (full model: $R^2 = 0.58$, $\chi^2_{35} = 19.2$, $P < 0.001$; Table 1). Overall, the model correctly classified 85% of the males as either early or late settling individuals according to UV chroma, body condition and fat content. Although UV chroma, body condition and fat content contributed to the model, UV chroma (Wald $\chi^2_{35} = 4.6$, $P = 0.03$; Figs 1, 2) was more important than body condition (Wald $\chi^2_{35} = 3.4$, $P = 0.07$) and fat content (Wald $\chi^2_{35} = 2.8$, $P = 0.10$).

We estimated the age class of each male as either second-year or after-second-year, and we found no significant difference in the ages of birds that acquired early versus late nestboxes in 1999 (Fisher's exact test: $P = 0.13$), 2001 ($P = 0.98$), or both years combined ($P = 0.31$).

Table 1. Means, standard deviations and sample sizes for plumage reflectance (brightness, UV chroma and hue), fat class and body condition of eastern bluebirds that acquired nestboxes early versus late in the spring

	Settlement speed	\bar{X}	SD	N
Brightness (%)	Early	0.27	0.85	17
	Late	-0.25	1.06	18
UV chroma	Early	0.41	0.86	17
	Late	-0.38	0.96	18
Hue (nm)	Early	-0.10	0.91	17
	Late	0.10	1.07	18
Body fat	Early	0.43	1.10	17
	Late	-0.45	0.59	18
Body condition	Early	0.37	0.42	17
	Late	-0.33	1.22	18

There were 2 years of data collected from two field sites in which the experiment was repeated and two settlement speeds (settlement in the first boxes erected in early spring or settlement in boxes added later in the spring). Data were transformed and standardized for year/site.

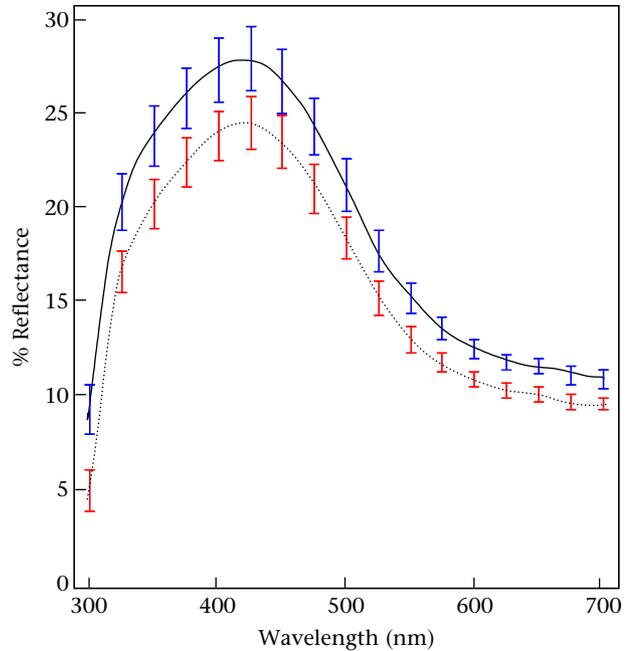


Figure 1. Average reflectance (with standard error bars at 25-nm intervals) of the UV-blue feathers of male eastern bluebirds that gained access to nestboxes earlier (solid line) and later (dashed line) in the spring of 2001.

In 1999 only, we measured annual reproductive success as the number of offspring fledged. Despite high predation rates (53% of the nests were depredated), more colourful males experienced greater reproductive success. Males that displayed brighter plumage and greater UV chroma fledged more offspring (Pearson correlation: $r_{16} = 0.51$,

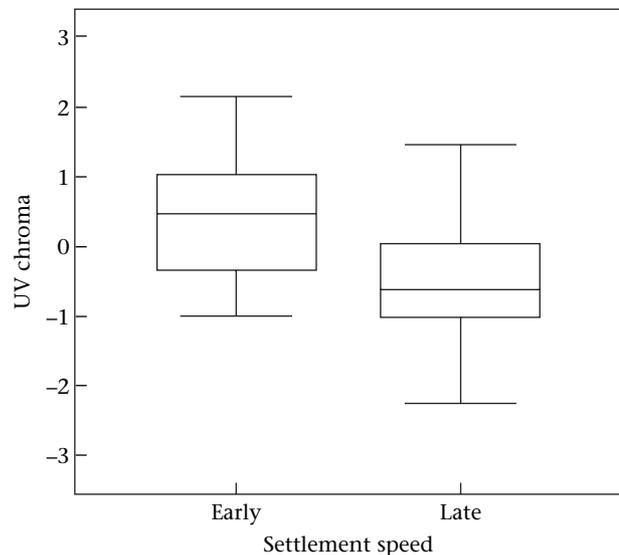


Figure 2. Box plots of UV chroma of male eastern bluebirds that acquired nestboxes that we erected earlier versus later in the spring. The line within each box represents the median colour score, the upper and lower borders of each box are the 25th and 75th percentiles, and the lower and upper bars are the 10th and 90th percentiles. Data are transformed and standardized for year and site.

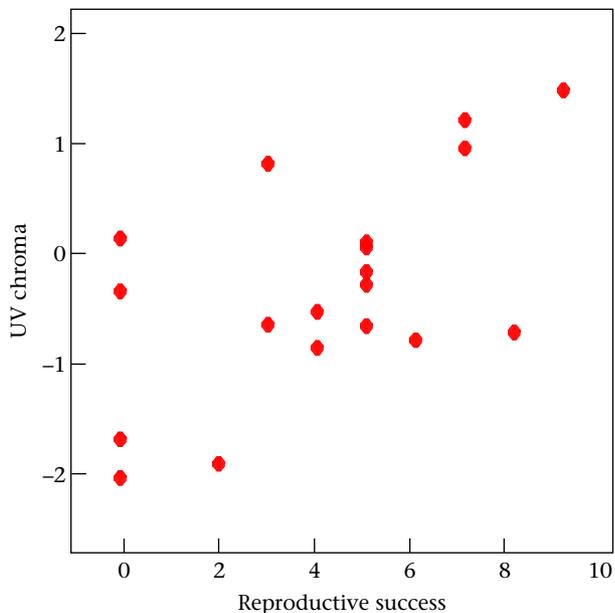


Figure 3. Relationship between UV chroma and reproductive success (number of offspring fledged) of male eastern bluebirds.

$P = 0.02$; $r_{16} = 0.58$, $P < 0.01$; Fig. 3). However, there was no relationship between hue and number of offspring fledged ($r_{16} = 0.12$, $P = 0.63$).

We were concerned that the colour differences between early and later settling males might be due to difference in the date on which the males were captured, allowing for more feather wear in one group than the other. To investigate whether plumage characteristics were likely to be affected by feather wear, we correlated plumage colour with date of capture. We found no consistent trends between day of capture and brightness (Pearson correlation: $r_{33} = -0.24$, $P = 0.17$), UV chroma ($r_{33} = -0.16$, $P = 0.37$), or hue ($r_{33} = 0.04$, $P = 0.80$).

At each study site each year, after the early spring nestboxes were erected, we observed many agonistic male–male interactions centred at the nestboxes. These interactions began with both males alternating between standing on the box, looking into the entrance of the nestbox, and displaying with their wings while chattering. Males often displaced each other at the box. In some cases, these agonistic interactions escalated to individuals wrestling on the ground and repeatedly attempting to peck at each other's head until one individual retreated. Because we captured males after they had attracted a mate and initiated a nest, however, we were unable to identify the winners and losers of these agonistic interactions except by which male eventually gained possession of the box.

Despite the intense competition for nest sites, many of the nestboxes that we erected in the early spring were not occupied by bluebirds prior to the placement of the late spring nestboxes (6 of 15 boxes in 1999, and 7 of 15 nestboxes in 2001). In both years at each site, however, all but two of the 13 unoccupied nestboxes remained unoccupied over the course of the breeding season. Thus, only 15% of the nestboxes that we erected early in the season became occupied after we erected the late spring

nestboxes. All unoccupied nestboxes tended to be close to forest edges and thus the habitat was probably unsuitable to eastern bluebirds.

DISCUSSION

Although plumage coloration is an important signal of social status in many species of birds, all previous studies of plumage colour and dominance have focused on coloration produced from pigments deposited in feathers, with more studies of melanin coloration (see Senar 1999 for review) than carotenoid coloration (McGraw & Hill 2000a, b; Pryke et al. 2001). The only evidence, to date, of the potential role of structural plumage coloration in male–male competition comes from blue grosbeaks, *Guiraca caerulea*. In the wild, brighter males defend larger territories of higher quality than do duller males (Keyser & Hill 2000). Moreover, in an experimental test of female mate choice based on relative male plumage coloration, female blue grosbeaks did not use male colour as a criterion in mate choice (Ballentine & Hill 2003).

Despite the fact that structurally based ornamental plumage is widespread across avian taxa, the role of structural coloration in male–male competition for access to territories has not been tested experimentally. Eastern bluebirds are a particularly appropriate study species for this question because males without a suitable nest cavity cannot attract a mate; therefore, males aggressively compete for access to nestboxes and male aggression plays a central role in the breeding biology of this species. In our experimental test, we found that the UV chroma of structural plumage colour predicted which males gained ownership of nest sites. Our study constitutes the first experimental evidence for a relationship between structural plumage colour and male competitive ability.

Our observation that both structural coloration and measures of individual condition predict male competitive ability in eastern bluebirds is hardly surprising. Success in male contests certainly depends on health and condition. Recent studies indicate that the production of structural plumage coloration is related to nutritional condition (Keyser & Hill 1999; Doucet 2002; McGraw et al. 2002; Johnsen et al. 2003) and viability (Sheldon et al. 1999). Furthermore, brood-size manipulations also show that structural coloration is sensitive to prior paternal reproductive effort, indicating that plumage colour is dependent on individual condition (unpublished data).

Thus, although there is mounting evidence that structural coloration is costly to produce, the associations between colour and other characteristics of the feather microstructure of individuals of a population have yet to be fully explored. The UV-blue of eastern bluebirds results from feather nanostructures in the spongy, medullary layer of feather barbs (Prum et al. 1999a). This layer is composed of a matrix of keratin rods and air vacuoles of varying shapes and sizes around a basal layer of melanin granules that surround a large air-filled nuclear vacuole (Auber 1957; Dyck 1971a). Research by Shawkey et al. (2003) indicates that variation in the reflectance properties of eastern bluebird coloration is determined by characteristics

of the keratin rods in the medullary layer of the feather barbs. Bluebirds that express more saturated UV-blue (chroma) have more keratin rods and keratin rods that vary less in size than duller males. This highly ordered arrangement could be difficult to produce, such that only the males in the best nutritional condition during moult are able to express the most brilliant coloration. Although variation in plumage brightness has not been explained by the structures within the medullary layer of the feather, it may be that brightness is determined by the thickness of the feather cortex or the number of barbules.

The reflectance measures of structural plumage in blue tits vary with seasonality, probably due to feather wear or the accumulation of dirt on the feather (Örnberg et al. 2002). The plumage of birds measured soon after moult show a greater shift in hue towards the UV, higher UV chroma and lower brightness than birds measured several months later in the year. Our data show that males who won access to the first available nestboxes were more colourful than the birds that settled later. If the UV chroma of eastern bluebirds were affected by seasonality in the same manner as in the blue tits, then UV chroma should have decreased with time. Although the birds who settled in the early group were captured, on average, 28 days before the birds who settled in the later available nestboxes, we found no clear relationships between day of capture and spectral characteristics in our study. Capture date was probably not related to plumage colour because there was, on average, only 1 month difference in the capture date of the two groups of males. The relationship between plumage colour and box acquisition appears to be driven by reliable signalling of male competitive ability via plumage colour and not due to differences in timing of capture of males in the two groups.

Age could also influence the competitive ability of eastern bluebirds either because of the effects of feather wear on the plumage or because older males may be better able to compete for access to limited resources. Because the rectrices of eastern bluebirds are not moulted in the postjuvenile moult (Pitts 1985) and, therefore, the rectrices of yearling males are 3–6 months older than those of after-second-year males, yearling males are likely to show more feather wear on their rectrices than older males. Although older males might be expected to be more competitive than younger males, older males in our study were not significantly more likely to acquire boxes earlier in the season. Thus, the relationship between plumage colour and box acquisition is probably driven by reliable signalling of male competitive ability via plumage colour rather than the effect of male competitive interactions on feather wear.

In many species, secondary sexual characters function both in male–male competition and as cues for female mate choice (review in Berglund et al. 1996). In eastern bluebirds, research indicates that females attain fitness benefits from mating with males who display brighter and more spectrally pure colour because those males provision offspring more and rear offspring that fledge at a greater mass (Siefferman & Hill 2003). Indeed, in the present study, we found that more colourful males fledged more offspring. Thus, it seems that more colourful males can win competitions for nest sites, invest more energy in

the feeding of offspring, and consequently, enjoy higher reproductive success. In eastern bluebirds, male competition may increase signal honesty by preventing low-quality males from acquiring social mates and, consequently, increase the intensity of sexual selection. It seems plausible that both male and female bluebirds assess plumage coloration of males (i.e. to assess an opponent and to assess a potential mate, respectively).

While we found strong correlations between colour display and success at acquiring resources, our investigation does not allow us to determine conclusively whether colour mediates the decision to escalate or retreat from a contest. Ultimately, experiments that manipulate plumage colour will be needed to test whether plumage colour is a true 'signal of status' (Rohwer 1977). Our observations indicate that structural plumage coloration is a condition-dependent trait that males could use to accurately assess the fighting ability of competitors. Our findings, along with other recent studies, show that structural plumage colour is a reliable indicator of male quality that can be used in both inter- and intrasexual signalling.

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