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Ornamental plumage coloration and condition are dependent on age in eastern bluebirds *Sialia sialis*

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Male eastern bluebirds *Sialia sialis* have striking ultraviolet (UV)-blue coloration on their heads, backs, rumps, wings, and tails and bold chestnut coloration on their breasts. These colored areas are ornaments that correlate with pairing date and reproductive effort, and thus probably influence the choice of mates by females. Such ornaments are expected to increase in color with age and body condition. We investigated the effects of age on body condition and the UV-blue and chestnut coloration of males over four years using both cross-sectional (comparing age classes) and longitudinal analyses (following individuals as they age). We found that both the body condition index and brightness of UV-blue rump coloration increased with age, while UV-blue tail plumage coloration increased between yearling and older males, and the chestnut breast coloration decreased in the oldest age class. The proximate mechanisms whereby individuals reliably signal age via rump brightness and tail coloration are probably different. Contour feathers, including rump feathers, are molted at approximately the same time in all age classes and are likely subject to the same production costs in all age classes. In contrast, the molt schedule of the tail and wing feathers differs between individuals of yearling and older age classes, with yearlings retaining wing and tail feathers for several months longer than adults. The relationship between tail color and age was probably, in part, a consequence of yearlings expressing tails that have increased feather wear and accumulation of dirt. In general, UV-blue coloration increased with age while chestnut plumage decreased with age, indicating that older individuals may tradeoff investing energy in structural and melanin ornaments. By assessing overall plumage coloration, female eastern bluebirds could estimate age class when choosing mates.

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Theory predicts that condition-dependent sexually selected characters honestly signal male quality (Zahavi 1975, Grafen 1990), and typically will be more developed in older individuals (Andersson 1994). If females prefer to mate with older males because old age signals good genes (Manning 1985), or because older males are in better physical condition and thus able to provide better resources (Marchetti and Price 1989), then females could use expression of ornamental traits to help them find older mates (Kokko 1998, Brooks and Kemp 2001, Proulx 2002). Studies of many species of animals have shown that mating success is correlated with age (Johnstone 1995), and female preferences for older males are common (Coté and Hunte 1993, Dunne and Cockburn 1999, Richardson and Burke 1999). In some species, females prefer more ornamented males that also tend to be older (Sundberg and Dixon 1996). In contrast to the extensive literature concerning female mating preferences relative to male ornamentation, fewer detailed studies have focused on how sexually selected traits change with age (but see Gil et al. 2001, Badyaev and Duckworth 2003).

When studying the effect of age on sexually selected traits, it is often helpful to combine longitudinal and cross-sectional approaches (Gil et al. 2001). The majority of studies use cross-sectional approaches, which compare the characteristics of different age classes in a particular year. Better but more difficult are longitudinal studies that follow individual animals across years. Because sexual selection theory predicts that male ornaments may show positive (Andersson 1994) or negative (Kokko 1998) correlations between survival and the expression of the trait, differential mortality may confound the results of a cross-sectional study (Endler 1986). Longitudinal studies have the advantage of following individuals as they age. Unless the data are standardized for year-to-year variation in the mean ornamentation of the population, however, longitudinal approaches can also be misleading. By using both methods, one can best determine the importance of age on ornamental traits.

Male eastern bluebirds *Sialia sialis* display bright UV-blue plumage on their back, rump, head, wings, and tails, and chestnut coloration on their breasts. Bluebirds are sexually dichromatic but do not exhibit delayed plumage maturation. Although eastern bluebirds are socially monogamous, females mated to younger males are more likely to cuckold their mates (Gowaty and Bridges 1991). Furthermore, in the sister species, the western bluebird *Sialia mexicanus*, females engage in more extra-pair copulations with older males (Dickinson 2001). In recent studies, we demonstrated that female eastern bluebirds gain fitness benefits from pairing with more ornamented males (Siefferman and Hill 2003). Male eastern bluebirds that exhibit more exaggerated plumage (brighter UV-blue plumage color and darker chestnut breast coloration) mate earlier in the breeding season, provide better parental care, and fledge larger offspring. Furthermore, we found that experimentally decreasing parental investment caused male eastern bluebirds to become brighter after the subsequent molt, indicating that structural coloration is a condition-dependent trait (Siefferman and Hill 2005a). Finally, the molt schedule of the tail and wing feathers differs between individuals of different age classes. Yearling bluebirds first acquire ornamental UV-blue structural plumage coloration on tail and wings during the nestling stage in the spring or summer (at about 11–15 days of age), and partial molt into their first ornamental body plumage (including breast and rump) during the autumn molt (Pitts 1985). Birds in their second year of life or older undergo a complete molt each autumn following the breeding season.

The aim of our study was to determine to what extent age influences plumage color and body condition in eastern bluebirds. We used a 4-year data set to asses whether birds increased in ornamentation and body condition with age, and to examine whether the relationships between different types of plumage color change with age class. We used both cross-sectional and longitudinal approaches to analyze our data.

Methods

Population monitoring and marking

We conducted this study in Lee County, Alabama (32°35′N, 82°28′W) from 1999–2002. We captured breeding males at nest boxes during the period that their mates were building nests and laying eggs (March–April). We marked each bird with a unique combination of three colored plastic bands and one U.S. Fish and Wildlife Service aluminum band. We estimated the age of all newly banded birds as either yearling (having undergone only one post-nestling molt), or in its 2nd or subsequent year based on the shape of the 10th primary feather (Pitts 1985). Furthermore, we knew the exact age of a subset of birds that were banded as nestlings on our field site. We refer to birds in their 1st year of life as "1st years", birds in their 2nd year of life as "2nd years", birds in their 3rd year of life as "3rd years", and birds in their 4th year of life as "4th years".

We used both the residuals of a regression of body mass on tarsus length and the ratio of body mass to tarsus length as indices of body condition. The results were very similar for the residual analyses and the ratio analyses, so only the results of the residuals of body mass on tarsus length are shown. Body-condition indices are thought to reflect variation in diverse aspects of the quality of organisms including health, nutritional status, and fat content (Brown 1996). The amount of body fat carried by individuals can change substantially with season and across a nesting cycle, however, so body condition indices must be used with caution (reviewed in Hayes and Shonkwiler 2001). For this study, our condition index appears to be a relevant measure of individual quality. We weighed and measured all individuals in early spring at the time of nest initiation, so we standardized all measures for season and point in the nesting cycle. Prior research with bluebirds in our population has shown that males in better body condition (heavier birds of given structural size) during early spring are better able to compete for limited nest sites (Siefferman and Hill 2005b), and females in better body condition lay eggs earlier in the year and provision offspring more often (Siefferman and Hill in press).

Color analysis

At time of capture, we collected 9 breast, 9 rump, and two outer tail feathers from each bird. Feathers samples were carefully plucked from the same location on all birds. The feathers were placed on black paper in a fashion that mimicked the way the feathers naturally lay on the bird. We stored the feathers in separate envelopes in a climate-controlled environment until spectrophometric analyses were conducted. One researcher (LS) recorded spectral data with an Ocean Optics S2000 spectrometer (range 250–880 nm; Dunedin, Florida, USA) using a micron fibre-optic probe at a 90-degree angle to the feather surface (see detailed methods in Siefferman and Hill 2003). For each individual, we recorded plumage coloration of the chestnut breast feathers and the UV-blue coloration from the rump feathers and two outer tail feathers.

Using spectral processing program (ColouR v1.7, Queens, Ontario), we summarized reflectance data by calculating three standard descriptors of reflectance spectra: UV-chroma, hue, and brightness. Brightness, or total amount to light reflected by the feather, is the summed reflectance from 300 to 700 nm. Chroma and hue were calculated differently for UV-blue and chestnut coloration because of the inherent reflective properties of the two colors. For the rump and tail feathers, UV-chroma, a measure of spectral purity, was calculated as the ratio of the UV reflectance (300–400 nm) to the total reflectance (300–700 nm). For the chestnut breast feathers, red-chroma was calculated as the ratio of the total reflectance in the red range (575–700 nm) to the total reflectance of the entire spectrum (300–700 nm). Hue is the principal color reflected by the feather. For structural coloration (rump and tail), hue was calculated as the wavelength at peak reflectance. Because hue (calculated as maximum slope) of the chestnut breast feathers expressed very little variation among males, we do not report hue for breast coloration. Unlike the analyses in Siefferman and Hill (2003), we analyzed the plumage color of the rump, tail, and breast feathers separately because 1) yearling and older birds molt tail feathers at different times, and 2) the UV-blue coloration of the rump and tail is produced by the feather nanostructure (Shawkey et al. 2003) while the chestnut coloration of the breast is caused by the deposition of melanin pigments (McGraw et al. 2004).

Statistical analysis

Non-normal data were transformed using $\log_{10}$ (brightness and hue) or arcsin (chroma). We found significant effects of year-to-year variation on all 8 color characters (ANOVA: Ps <0.001), so we standardized the color and body condition data for each year to a mean of zero and standard deviation of 1. To analyze the plumage coloration of each body region, we used principal components analyses (PCA) based on correlation matrices of standardized plumage characteristics. This analysis allowed us to both reduce the data to a limited number of variables and to elucidate the co-linearity in our spectral measures.

For the cross-sectional analysis, we only used data from one year (2002) because we knew the exact age of the greatest number of birds in this year. We used an analysis of variance to determine whether body condition differed according to age class. We then explored the importance of both age and body condition on plumage coloration. To do this, we used an analysis of covariance with age as the fixed factor, body condition as the covariate, and plumage color as the dependent variable.

For the longitudinal analysis, we used paired t-tests to determine whether individuals increased in ornamentation and body condition between ages 1 and 2 years, age 2 and >2 year, and age 1 and >2 year. T-tests were 1-tailed because, by first conducting cross-sectional analyses, we formed predictions that structural color would increase with age and melanin color would decrease with age.

Finally, to understand the relationships among the plumage variables, we used an analysis of covariance to test for interaction affects of age (first year and older) and plumage color on other plumage color variables. We analyzed the relationships between plumage variables separately for younger and older birds when the interaction was significant.

Results

In 2002, we measured 36 1st-year-males, 30 2nd-year-males, and 19 $>$2nd year-males (3rd or 4th year). Of all the males captured over the course of four years, 34 were captured in both their 1st and 2nd years, 30 were captured in both their 2nd and $>$2nd years, nine were captured in both their 1st and $>$2nd years. Because we failed to measure the body condition and collect tail feathers from a few individuals, samples sizes vary.

Principal components analysis

The hue and UV-chroma of the rump coloration contributed strongly to the 1st principal component of rump color, explaining 55.7% of the rump plumage color variation (Table 1). The 2nd principal component of rump coloration was heavily dependent on plumage brightness and explained an additional 34.8% of rump plumage variation. Overall, 90.5% of the variation in rump color was explained by the 1st and 2nd principal component. Both the brightness and red chroma of chestnut coloration contributed highly to the 1st principal component of breast ornamentation whose eigenvalue explained 74.5% of the breast plumage color variation. Hue and UV-chroma of blue tail coloration contributed strongly to the 1st principal component of tail color, which explained 60.0% of the tail plumage color variation.

Table 1. Eigenvectors for the 1st and 2nd principal components (PC) of principal component analyses (PCA) preformed on 3 color characters of rump color, the 1st PC for a PCA performed on 3 color descriptors of tail color, and the 1st PC for a PCA preformed on 2 color descriptors of breast color of male eastern bluebirds. These data have been transformed and standardized for year.

Data type	PC1	PC2
Rump coloration		
Rump brightness	0.06	0.99
Rump chroma	0.92	0.14
Rump hue	−0.91	0.21
Tail coloration		
Tail brightness	0.22	
Tail chroma	0.93	
Tail hue	−0.91	
Breast coloration		
Breast brightness	−0.86	
Breast chroma	0.86	

Cross-sectional analysis

Body condition increased significantly with age class (ANOVA: $F_{2,80}=8.2$, $R^2=0.17$, $P=0.001$; Fig. 1a; Table 2). Post hoc comparisons (Tukey HSD) showed that body condition significantly increased from 1st to 2nd year ($P=0.01$) and from 1st to >2nd year ($P<0.001$). Because we were interested in the possible influences of both age and body condition on plumage traits, we used an analysis of covariance with age as the fixed factor and body condition as the covariate to test for the affect of age and body condition on plumage coloration. Moreover, we first tested for an interaction between age and body condition on plumage characteristics. There was no significant interaction between age and body condition on the rump UV chroma/hue (PC1; ANCOVA, interaction: $F_{2,77}=0.30$, $P=0.75$), and rump UV chroma/hue (PC1) showed no significant difference between age classes (ANCOVA, Full model: $F_{3,79}=2.2$, $R^2=0.08$, $P=0.1$). There also was no significant interaction of age and body condition on rump brightness (PC2; ANCOVA, interaction: $F_{2,77}=0.35$, $P=0.70$). The brightness of the rump (PC2) differed among age classes (ANCOVA, Full model: $F_{3,79}=3.8$, $R^2=0.13$, $P=0.01$; Fig. 1b), but body condition was not a significant predictor of rump brightness ($F_{1,79}=1.3$, $P=0.25$). Post hoc comparisons between the rump brightness of males in the three age classes showed a significant increase from 1st to >2nd year ($P=0.01$). There was also no significant interaction of age and body condition on tail coloration (PC1; ANCOVA interaction: $F_{2,75}=0.77$, $P=0.47$). Tail coloration differed significantly with age class (PC1; ANCOVA Full model: $F_{3,77}=4.8$, $R^2=0.16$, $P<0.01$; Fig. 1c), yet body condition was not a significant predictor of tail coloration ($F_{1,77}=1.2$, $P=0.27$). Post hoc comparisons of the tail coloration of males in the three age classes showed a significant increase from 1st to 2nd year ($P=0.01$) and from 1st to >2nd year ($P=0.01$). There was no significant interaction of age and body condition on breast coloration (PC1; ANCOVA, interaction: $F_{2,75}=0.12$, $P=0.89$). The melanin-based breast coloration decreased significantly with age class (PC1; ANCOVA Full model: $F_{3,77}=7.2$, $R^2=0.22$, $P<0.001$; Fig. 1d), and body condition was not a significant predictor of breast coloration ($F_{1,77}=0.1$, $P=0.77$). Post hoc comparisons of breast color revealed that >2nd year birds were less ornamented than either 1st year birds ($P<0.001$) or 2nd year birds ($P<0.001$).

Longitudinal analysis

The comparison of the plumage characteristics of the same birds as they aged confirmed the patterns found in the cross-sectional analysis. Birds were in better body condition in their 2nd year than in their 1st year ($t=2.14$, $n=31$, $P=0.02$; Table 3), in their >2nd year than in their 2nd year ($t=2.3$, $n=30$, $P=0.01$), and in their >2nd year than in their 1st year ($t=3.24$, $n=8$, $P<0.01$). Rump UV chroma/hue (PC1) did not increase with age; birds did not differ from year 1 to year 2 ($t=0.26$, $n=34$, $P=0.40$), from year 2 to year >2 ($t=0.45$, $n=30$, $P=0.32$), nor from year 1 to year >2 ($t=1.27$, $n=8$, $P=0.12$). Although rump brightness (PC2) did not increase significantly from year 1 to year 2 ($t=0.91$, $n=34$, $P=0.17$), it did increase significantly from year 2 to year >2 ($t=2.08$, $n=30$, $P=0.02$), and tended to increase from year 1 to year >2 ($t=1.64$, $n=9$, $P=0.07$). In accordance with the cross-sectional analysis, birds displayed more colorful tails in their 2nd than in their 1st year ($t=3.61$, $n=30$, $P=0.001$), tended to be more colorful in their >2nd than in their 1st year ($t=1.73$, $n=6$, $P=0.07$) but did not display more colorful tails in their 3rd than in their 2nd year ($t=-0.57$, $n=29$, $P=0.29$). For breast coloration, the longitudinal results were similar, but not identical, to the results obtained for the same variable in the cross-sectional analysis. Birds did display less colorful breasts in the oldest age class (>2nd) than in their 2nd year ($t=-1.66$, $n=30$, $P=0.05$), but there were no significant differences between either 2nd and 1st year birds ($t=0.48$, $n=34$, $P=0.31$) or >2nd and 1st year birds ($t=0.10$, $n=9$, $P=0.47$).

Relationships among plumage measures

In the following analyses, we were interested in the relationships among plumage traits and whether those relationships changed with age. There was no significant interaction between age class and the relationship between rump chroma/ hue (PC1) and tail coloration (PC1; ANCOVA, interaction: $F_{1,79}=1.9$, $P=0.17$). Rump chroma/ hue (PC1) and tail coloration (PC1)

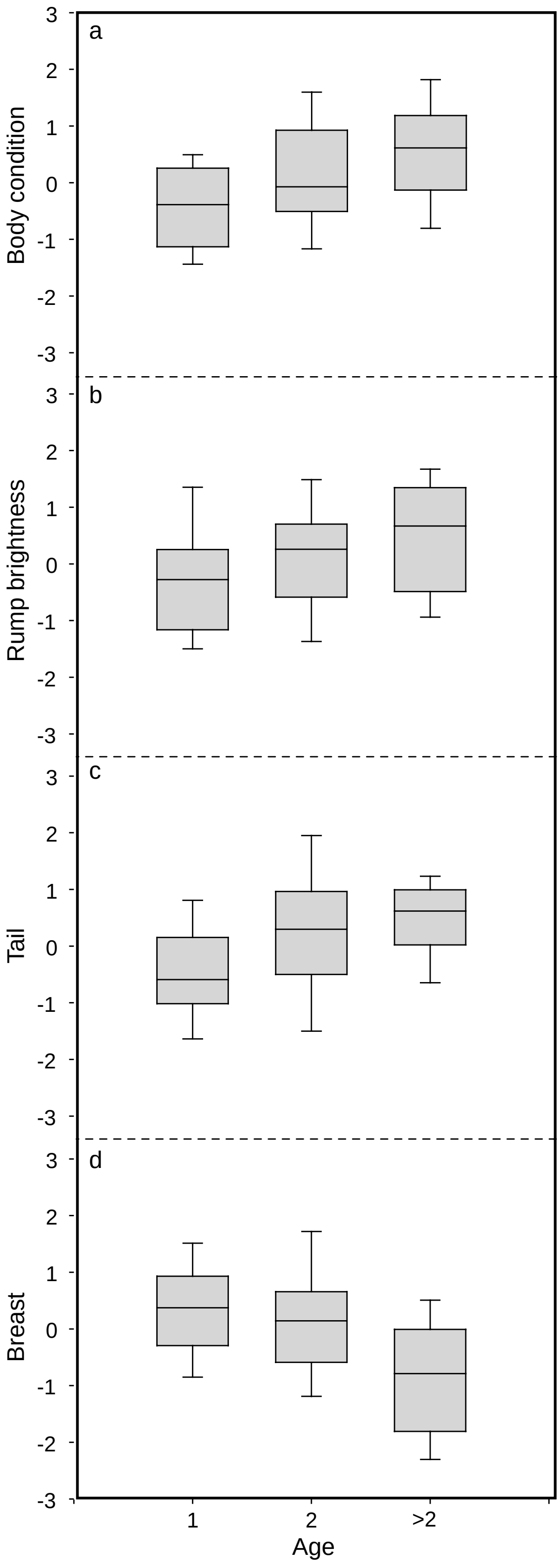

Fig. 1 (*Continued*)

were significantly positively related (Regression: $R^2 = 0.35$, $n = 82$, $P < 0.001$) such that birds with rumps that expressed greater UV chroma and left-shifted hues tended to have more colorful tails. There was also no significant interaction between age class and the relationship between rump brightness (PC2) and tail coloration (PC1; ANCOVA, interaction: $F_{1,79} < 0.01$, $P = 0.99$), and the relationship between rump brightness (PC2) and tail coloration (PC1; Regression: $R^2 = 0.01$, $n = 82$, $P = 0.28$) was not significant. The interaction of age class and the relationship between rump chroma/ hue (PC1) and breast coloration (PC1) was significant (ANCOVA, interaction: $F_{1,79} = 4.1$, $P < 0.05$), thus the relationships between rump chroma/hue and breast coloration changed between young and old birds. For yearling birds, rump chroma/ hue (PC1) and breast plumage (PC1) were positively related ($R^2 = 0.14$, $n = 34$, $P = 0.03$), but for older birds ($>$1y) this relationship was not significant ($R^2 = 0.02$, $n = 47$, $P = 0.38$). The interaction between age and the relationship between rump brightness (PC2) and breast coloration (PC1) was also significant (ANCOVA, interaction: $F_{1,79} = 4.1$, $p < 0.05$; Fig. 2). For yearling birds, rump brightness (PC2) and breast plumage (PC1) were positively related ($R^2 = 0.02$, $n = 34$, $P = 0.05$), but for older birds ($>$1y) there was a stronger negative relationship ($R^2 = 0.15$, $n = 47$, $P < 0.01$). There was no significant interaction between age class and the relationship between tail coloration (PC1) and breast coloration (PC1; ANCOVA, interaction: $F_{1,78} = 1.7$, $P = 0.19$), and no significant relationship existed between tail coloration (PC1) and breast coloration (PC1; Regression: $R^2 < 0.01$, $n = 81$, $P = 0.63$).

Discussion

By studying the effects of age on the expression of structural and melanin plumage in male eastern bluebirds, we investigated whether these two types of plumage ornamentation can signal age. We found evidence that the index of body condition, and both

Fig. 1. Box-plots for male eastern bluebirds of ages 1 year, 2 years, or older than 2 years of a. body condition (standardized residuals of a mass to tarsus regression) where higher scores correspond to birds in better body condition (larger mass relative to skeletal size), b. brightness of the rump plumage (PC2) where higher principal component scores correspond to more ornamented birds (greater total reflectance), c. UV chroma/hue of tail plumage (PC1) of male eastern bluebirds where higher principal component scores correspond to more ornamented birds (greater UV chroma and more left shifted hue), and d. chestnut coloration of breast plumage (PC1) where higher principal component scores correspond to birds with more ornamented melanin plumage (darker color and greater red chroma). The line within each box represents the median color score, the upper and lower borders of each box are the 25th to 75th percentiles, and the lower and upper bars are the 10th and 90th percentiles.

Table 2. Cross-sectional comparison of body condition and color characteristics of male eastern bluebirds in 2002 at ages 1, 2, >2 years. For all principal components analyses, larger PC scores correspond to greater ornamentation.

Character	1 year		2 year		>2 year		
	Mean (±SD)	n	Mean (±SD)	n	Mean (±SD)	n	F
Body condition	−0.43±0.9	36	0.17±1.0	29	0.59±0.9	18	5.6**
Rump color PC1	−0.21±0.9	36	−0.02±1.2	30	0.43±1.0	19	1.9
Rump color PC2	−0.30±0.9	36	0.05±1.0	30	0.50±1.0	19	3.4*
Tail color PC1	−0.47±0.8	34	0.25±1.2	30	0.45±0.6	19	4.8**
Breast color PC1	0.34±0.9	34	0.15±1.1	30	−0.87±1.0	19	6.6**

* = $P < 0.05$, ** = $P < 0.01$.

structural and melanin plumage are sensitive to age. Older birds were in better body condition, expressed more colorful structural plumage, and less ornamented melanin coloration. Furthermore, we found that rump brightness and breast plumage were negatively correlated, suggesting that older eastern bluebirds may experience tradeoffs between producing structural and melanin coloration.

The cross-sectional analysis and longitudinal analyses showed that UV-blue coloration and body condition increased with age. Older birds produced more colorful structural plumage and were in better body condition during the breeding season than younger birds, so older birds may be honestly signaling their ability to provide high quality resources to potential mates. In this study, we measured body condition in the spring, at the beginning of the breeding season rather than in the fall, during molt, and this discrepancy may explain why body condition did not covary with structural coloration, independently of age. Although the cost of structural plumage brightness is not yet fully understood, evidence suggests that producing bright plumage color is energetically demanding. Indeed, in a past experiment, we showed that increasing paternal effort negatively affects the ability of males to produce colorful UV-blue plumage during the following molt (Siefferman and Hill 2005a). Moreover, in blue grosbeaks (*Guiraca caerulea*; Keyser and Hill 1999), blue-black grassquits (*Voliatinia jacarina*; Doucet 2002), and brown-headed cowbirds (*Molothrus ater*; McGraw et al. 2002) production of structural plumage coloration is correlated with individual condition during molt.

In the cross-sectional analysis we found that the UV-blue structural plumage coloration of the tails of eastern bluebirds increased significantly between 1st year and older birds. These results were corroborated in the longitudinal analysis; males displayed significantly duller tail color in their 1st year of life. Although tail coloration is probably affected by condition during molt, the color difference between tails of yearling and older birds may also be driven by the difference in the molt schedule of yearling and older birds. Yearling birds grow tail feathers while still in the nest (between May and August) and then retain these feathers through their first breeding season. In contrast, older birds molt tail feathers in the autumn (September to October). Because of this molt schedule, yearling birds display tail feathers that are 2–6 months older than the tail feathers of older birds. Örnborg et al. (2002) found that the reflectance measures of structural plumage in blue tits *Parus caeruleus* varied over the course of many months, probably due to feather wear or the accumulation of dirt on the feather. Birds measured soon after molt exhibited hues shifted more towards the UV, had higher UV chroma, and were less bright than birds measured later in the year. If feather wear or accumulation of dirt, oils, or fat reduce the overall plumage coloration of tail feathers in eastern bluebirds, 1st-year birds should be less ornamented than after-1st-year birds simply due to feather age. The tail coloration data are consistent with the hypothesis that accumulation of dirt or feather wear dulls the signal of 1st year birds.

In male eastern bluebirds, both the UV-blue and chestnut plumage coloration are sexually selected traits.

Table 3. Longitudinal comparison of body condition and plumage characters between the same males at 1 and 2 years, 2 and >2 years, and 1 and >2 years of age. Data has been transformed and standardized for year. For all principal components analyses, larger PC scores correspond to greater ornamentation.

Character	1 year	2 year		2 year	>2 year		1 year	>2 year	
	X (±SD)	X (±SD)	n	X (±SD)	X (±SD)	n	X (±SD)	X (±SD)	n
Body condition	−0.19±1.1	0.13±0.9	31*	0.07±1.0	0.46±1.0	30**	0.09±0.7	1.47±1.0	8**
Rump color PC1	−0.05±0.9	−0.01±1.1	34	0.27±1.0	0.32±1.0	30	0.46±1.4	0.78±1.0	9
Rump color PC2	−0.21±0.9	−0.04±1.0	34	−0.23±1.0	0.27±0.9	30*	−0.18±0.8	0.42±0.7	9
Tail color PC1	−0.40±1.0	0.43±1.2	30**	0.29±1.0	0.16±1.0	29	−0.39±1.2	0.79±0.8	9
Breast color PC1	0.09±1.1	0.20±0.9	34	0.15±1.1	−0.28±1.2	30*	−0.41±1.2	−0.39±0.9	6

* = $P < 0.05$, ** = $P < 0.01$.

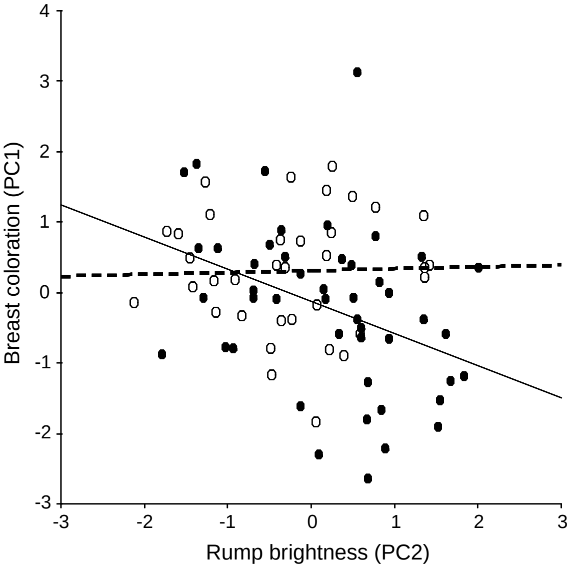

Fig. 2. The relationships between rump brightness (PC2) and breast coloration (PC1) in young (1yr; open circles, dashed line) and older (> 1yr; solid circles, solid line) male eastern bluebirds. Higher principal component scores correspond to birds with more ornamented structural (rump plumage displaying greater total reflectance) and melanin plumage (darker color and greater red chroma). The relationship becomes strongly negative in older birds.

Expression of both color displays are related to parental effort and reproductive success (Siefferman and Hill 2003). Our data demonstrates, however, that melanin plumage coloration was influenced by age class in a manner opposite from our predictions- birds in the oldest age classes were less ornamented. In older birds, we also found that melanin plumage ornamentation was significantly negatively related to rump brightness. This negative covariance between ornamental traits suggests that birds experience a tradeoff between investing energy towards structural and melanin ornamentation as they reach the older age classes. Multiple sexually selected ornaments have traditionally been expected to be positively correlated with each other (Kodric-Brown and Brown 1984). If allocation of energy is necessary for the production of both types of plumage coloration, however, negative correlations could arise (Andersson et al. 2002). Alternatively, the importance of having dark melanin plumage may decrease with age. Ultimately, to really understand why expression of chestnut breast coloration decreases with age, we need experimental studies of the function and proximate control of this ornamental coloration.

It also remains uncertain whether the structural coloration of eastern bluebirds functions primarily in male-male interaction, in female mate-attraction, or in both. It seems likely that female bluebirds use male UV-blue plumage color as an indirect age indicator when selecting mates, since older males generally are more brightly colored than younger males and females seem to prefer older mates (Gowaty and Bridges 1991). By assessing the overall plumage color of males, females should be better able to choose males who provide superior resources. Likewise, potential competitors could make more informed decisions during male-male competitive interactions for breeding resources. Although we have identified a link between age, condition, and plumage coloration in this study, it will be important in future research to investigate the physiological allocation towards and potential tradeoffs between multiple traits in eastern bluebirds.

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