

# Structurally based plumage coloration is an honest signal of quality in male blue grosbeaks

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We investigated the signaling function of blue plumage in male blue grosbeaks (*Guiraca caerulea*) to determine if structurally based coloration may act as a reliable signal of quality to conspecifics. Blue plumage results from the microstructure of feather barbules rather than from pigment granules, and thus it is possible that structurally based plumage ornaments may function differently from sexually selected ornamental coloration that is pigment based. The plumage of male blue grosbeaks reflects maximally in the blue-ultraviolet range, so most variation in plumage coloration among males is invisible to human observers. In previous research, we showed that increased area of blue plumage on the body is associated with a shift in the wavelength of maximum feather reflectance toward the ultraviolet and with high intensity of light reflected at that maximum, and that extreme expression of the male ornament is condition dependent. These observations suggest that blue plumage may be an honest advertisement of male quality. We tested this hypothesis in a wild population of blue grosbeaks. We quantified male quality in three broad categories. (1) Physical condition was assessed from subcutaneous fat deposits, ectoparasite load, and body size. (2) Territory quality was assessed from territory area, prey abundance, and predation risk. (3) Paternal investment was assessed from male feeding rate. We found that the bluest males have the largest body size, maintain the largest territories with the greatest prey abundance, and feed nestlings in the first nest of the season at the highest rates. We conclude that structurally based plumage coloration functions as an honest, intraspecific signal of quality. *Key words*: honest advertisement, mate choice, reliable signaling, sexual selection, structural color, ultraviolet reflectance. [*Behav Ecol* 11:202–209 (2000)]

Conspicuous secondary sexual characteristics are a prominent feature of males in many species of animals. Enormous body size in elephant seals (*Mirounga* sp.), elaborate tail fans in male peacocks (*Pavo cristatus*), and brilliant colors in guppies (*Poecilia reticulata*) are familiar examples. The honest advertisement model of sexual selection proposes that variation in these secondary sexual characteristics is maintained through intraspecific interactions. First, the model proposes that there is competition for access to mates either through intrasexual interactions or intersexual mate choice (Darwin, 1871). Second, these interactions are mitigated by ornamental traits such that individuals bearing the most extreme expression of the traits have increased mating success (Darwin, 1871; Kirkpatrick, 1982). Third, expression of the ornament depends on the condition of the bearer and covaries with other measures of individual quality (Andersson, 1986; Hamilton and Zuk, 1982; Kodric-Brown and Brown, 1984; Zahavi, 1975). Fourth, this covariance allows conspecifics to assess mate quality accurately during mating interactions (Hill, 1996; Kodric-Brown and Brown, 1984).

To make a strong inference about how an ornament functions in a given species, it is important to document all elements of the reliable signaling model. One needs to know how the ornament varies, what maintains this variation, what is the information content of the signal, and whether it is used in intraspecific interactions. In several well-studied systems (see general review by Andersson, 1994), all parts of the model have been carefully addressed. For example, in house finches (*Carpodacus mexicanus*), male plumage varies from yellow

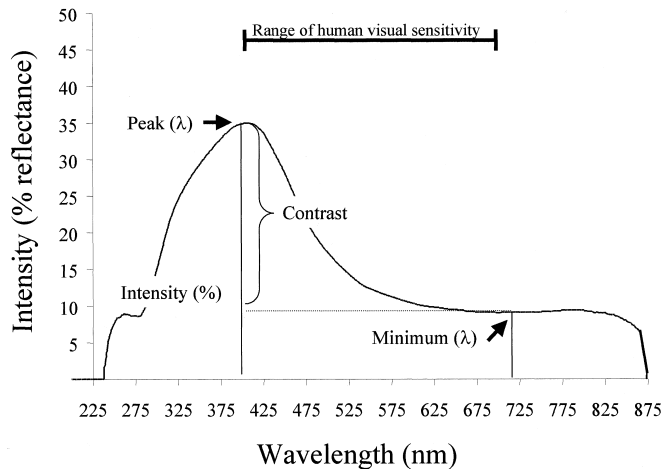
to red, and this variation depends on nutritional condition and endoparasite load (Brawner, 1997; Brush and Power, 1976; Hill, 1992; Hill and Montgomerie, 1994). Females preferentially mate with the reddest males (Hill, 1990, 1991, 1994; Hill et al., 1999), which have the highest overwinter survival rate (Hill, 1991) and feed incubating females more than duller males (Hill, 1991). In another example, female ring-necked pheasants (*Phasianus colchicus*) choose mates based on male spur length, and mating with long-spurred males increases female reproductive success (von Schantz et al., 1989). Spur length is associated with major histocompatibility complex genotype, which suggests an association between male immune response and display of ornamental spurs (von Schantz et al., 1996). Spur length is also positively correlated with male viability and offspring survival (von Schantz et al., 1994). Similar examples of female choice for reliable signals of quality can be found for guppies (*P. reticulata*; e.g., Houde, 1997; Houde and Torio, 1992; Kodric-Brown, 1985) and barn swallows (*Hirundo rustica*; Møller, 1994).

In the examples presented above, the ornamental trait under consideration is either a physical structure such as a long tail or a pigment-based color patch. Another class of ornamental traits consists of patches of color that are derived from the microscopic structure of the colored region rather than endogenous pigments. Such traits, referred to as structurally based colors, are found in a wide variety of taxonomic groups including arthropods, fish, and birds (Auber, 1957; Fox, 1976). Structural ornaments have been little studied, particularly in birds, perhaps because human observers perceive little variation in these ornaments (Borgia and Collis, 1990; Hunt et al., 1998). However, growing interest in the function of ultraviolet vision in birds has led researchers to look for “cryptic” ultraviolet signals in plumage (Andersson, 1996; Bennett and Cuthill, 1994; Burkhardt, 1989). Several species show variation in short-wavelength plumage reflectance, and

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**Figure 1**  
Representative reflectance spectrum of male plumage. The range of human visual sensitivity is 400–700 nm. Plumage variables extracted from spectral data include peak wavelength (designated  $\lambda$  and measured in nm), intensity (reflectance at peak as a percentage of a 100% reflective white standard), and contrast (difference between maximum and minimum intensity).

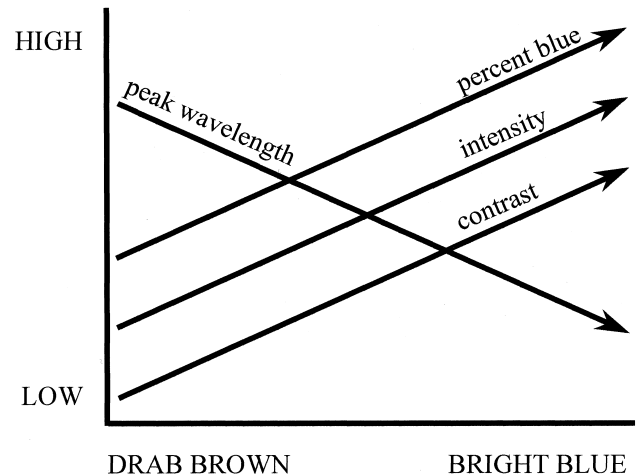
females of some of these species prefer males with the most extreme ultraviolet coloration (Andersson and Amundsen, 1997; Hunt et al., 1998).

Our recent work with a wild population of blue grosbeaks (*Guiraca caerulea*) documented extensive variation among males in expression of a structural, blue-ultraviolet ornamental trait (Keyser and Hill, 1999). In addition, we found a positive correlation between phenotypic expression of blue plumage and nutritional condition during molt (Keyser and Hill, 1999). Thus, a mechanism is in place whereby the signal is kept “honest” and suggests that ornamental plumage may function as an honest advertisement in this species. If male plumage acts as a signal to conspecifics, it is important to identify what information the ornament conveys.

In this study, we measured male quality in the field and calculated the correlation between several quality measures and male plumage characteristics. We quantified body size, current physical condition, territory size, prey availability, nest predation risk per territory, and male parental investment. We predicted that male plumage ornamentation would be positively correlated with quality measures. All of these have the potential to influence, directly or indirectly, female fitness and thus make female choice of the bluest males adaptive (Searcy, 1979). Additionally, significant correlations of body size, current physical condition, or territory size with ornamentation could suggest a potential role for plumage ornamentation in male–male competition. If fine-scale variation in a structural ornament correlates with male quality measures, it would provide further support for the universal applicability of honest signaling theory to ornamental traits in animals.

## METHODS

We studied a color-banded population of blue grosbeaks in Lee County, Alabama, USA, during the breeding seasons (April–August) of 1997 and 1998. The study site consisted of a series of agricultural fields (either planted in cotton, wheat, or used as pasture) surrounded by secondary growth forest and patches of recently clear-cut forest. Our efforts centered on two large (111 ha and 73 ha) and two small (11 ha and 30 ha) fields in 1997. In 1998, the two small fields were dropped from the study due to low density of blue grosbeaks,



**Figure 2**  
Schematic diagram of the relationships between the four plumage variables measured (summarized from Keyser and Hill, 1999). Peak wavelength, percent blue, and intensity are combined in breast and rump blueness scores for each male.

and a third large field (94 ha) was added. All of these fields were within a few kilometers of one another. However, blue grosbeaks are exclusively early-successional species, and territories established by males included clear-cuts, pastures, planted fields, and especially shrubby hedgerows and field edges. Birds were never heard or observed more than about 75 m into the forest around the fields. Once birds settled onto breeding territories, we did not observe them moving from one field to another.

Birds were captured in mist nets and Potter live-traps baited with sunflower seeds early in the season. Each individual was marked with a unique combination of colored leg bands and an aluminum U.S. Fish and Wildlife service band. In 1997, we captured 31 males, and of these, 20 remained in the study area and established breeding territories. In 1998, we captured 34 males, and 24 established breeding territories. Out of these 24, 7 males had also held territories during 1997.

At the time of capture, we collected feather samples for spectrophotometric analysis and took detailed plumage information from each male ( $n = 65$  for both years combined). We measured four plumage variables on the breast and rump region of each individual: percent blue, peak wavelength, intensity, and contrast (for detailed methods, see Keyser and Hill, 1999). Percent blue refers to the percentage of blue plumage on each body region and was estimated visually. This measure is highly repeatable among observers ( $r = .96$ ). The other three variables were obtained from reflectance spectra taken from the two body regions (see Figure 1 for representative spectra and plumage variable explanations). Spectral data provide an objective way to quantify color (Cuthill et al., 1999; Endler, 1990). Peak wavelength is the wavelength at which the plumage is maximally reflective and is an estimate of the hue or color principally reflected by the feathers. Intensity is the amount of light reflected at the peak wavelength and is a measure of the brightness of the color. Contrast is measured as the difference in intensity between the wavelength of maximum reflectance and the wavelength of minimum reflectance. A thorough investigation of plumage variation in male blue grosbeaks is presented elsewhere (Keyser and Hill, 1999); however, the relationship between various elements of plumage variation is summarized in Figure 2. In general, the bluest male grosbeaks have (1) a high proportion of blue feathers in the body plumage, (2) short peak wave-

lengths (sometimes into the ultraviolet range), (3) high intensity, and (4) high contrast.

To simplify our analyses, three plumage variables were summarized in a blueness score for each male (for rationale, see Keyser and Hill, 1999). Percent blue and intensity were ranked such that the male with the highest value received the highest rank. Peak wavelength was ranked in the opposite manner, the lowest peak wavelength yielding the highest rank. We excluded the contrast value from the blueness score because it is directly dependent on intensity. We calculated average rank for each male. Males captured in 1997 ( $n = 31$ ) were ranked separately from those captured in 1998 ( $n = 34$ ). Use of this blueness score dramatically reduced the number of statistical comparisons we made and equally weighted the information content of the individual plumage variables. If, and only if, a significant association was found between blueness and a quality variable, then we reanalyzed the data using the four plumage variables separately to determine if any single component of blue plumage was contributing disproportionately to the statistical pattern.

Previous work showed that the expression of plumage blueness is partially condition dependent (Keyser and Hill, 1999), and our intent was to investigate the potential information content of ornamental plumage in this species. To that end, we measured several male attributes (quality measures) that could be important to females selecting mates or to other males assessing the competition. These were body size, current physical condition, territory size, territory quality, and male parental care. Detailed methods are described below.

#### Data analysis

Many of the variables we measured were non-normally distributed, so nonparametric statistical tests were used in all cases unless otherwise stated. In the first set of analyses, we calculated the Spearman rank correlation between blueness score and the quality measure. This was done for the breast and rump blueness scores separately. If a quality measure was significantly correlated with blueness, we calculated a second set of correlations between that variable and the four individual plumage variables (percent blue, peak wavelength, intensity, and contrast).

#### Body size and current physical condition

At the time of capture, we made standard morphological measurements of tarsus length, wing chord length, and mass. Although individuals were only measured once per year, they were all measured within the same window of time. In 1997, all but five males were captured between April 22 and May 24, and in 1998, all males were captured between April 30 and May 29.

We scored several measures of physical condition in the field. Subcutaneous body fat was scored on an eight-point scale (Ralph et al., 1993). Feather lice abundance on primary feathers of the right wing was scored on a five-point scale: 0—no lice, 1—occasional lice, 2—many lice along rachis of some feathers, 3—nearly every feather with hundreds of lice, 4—all feathers with hundreds to thousands of lice. Intensity of avian pox infection was scored on a four-point scale: 0—no lesions, 1—one lesion, 2—two lesions, 3—three or more lesions.

#### Territory size and quality

To map territories, field technicians searched daily (approximately 0500–1100 h from April through August) for each banded male. Usually, every bird was located every day. When a bird was sighted, we marked its location and movements on

a map of the study area. We also noted consistently used song perches and delineated the boundary areas where male–male conflicts occurred. We used a minimum polygon method to connect areas of major activity for each male territory (Mohr, 1947). Males occupied a discrete area throughout the breeding season with little or no shifting of boundaries. Territory area was calculated from polygons plotted on maps traced from aerial photos.

During 1998 we assessed the availability of suitable prey by sweep-net sampling 100-m transects weekly from mid-May to mid-June. Each male's territory contained from one to three transects. These transects were located within grassy strips along the edges of agricultural fields and pastures. Each transect was sampled by pacing out 100 m and swinging the net 100 times such that it came into contact with the vegetation. Focal animal observations conducted during 1997 confirmed that adult grosbeaks preferentially forage along field edges when feeding nestlings, and they do not appear to leave the territory to forage. Males spent 55% of foraging time in field edges and pasture, and females spent 60% of time in these habitats (foraging time based on ~15 h of direct observations). Since orthopterans were the primary prey items fed to nestlings (as identified from video cameras at nests; Keyser and Hill, unpublished data), orthopterans were separated from sweep samples, counted, and weighed.

Nest predation can cause wide variation in reproductive success, thereby acting as a strong selective pressure (Hill, 1988; Martin, 1995; Ricklefs, 1969). If predation risk varies deterministically from territory to territory, it is possible that plumage ornamentation could signal the ability of a male to hold a territory with relatively low predation risk. Alternatively, bright males may attract the attention of predators and suffer increased predation risk. To test these hypotheses, we fit a logistic regression model to predict the probability of nest predation from male plumage blueness:

$$\ln\left(\frac{p_i}{1-p_i}\right) = b_0 + b_1x, \quad (1)$$

where  $p_i$  is the probability of a successful nesting attempt and  $x$  is the blueness score of the attending male at that nest.

#### Paternal investment

Video cameras set up at nests were used to assess whether bright males provided superior parental care. These miniature cameras (Fuhrman Diversified, Inc., Seabrook, Texas) can be placed close to active songbird nests using a camouflaged, articulated arm attached to nearby branches. They are capable of recording for 24 h on a single T120 VHS videocassette, and an infrared illuminator within the camera housing allows taping through the night (for description of the camera system, see Thompson et al., 1999). We placed cameras at active nests after nestlings had hatched; battery and videocassette were changed daily. The camera was removed when nestlings were 9–12 days old. These data were collected during 1998 only. From the video tapes we calculated male feeding rate per hour (from 0600 to 2000 h).

## RESULTS

#### Body size and current condition

When analyzing the association between blueness and body size, data were collected from all males captured in 1997 and 1998. We included the seven males that were captured in both years only once in the analysis, and we used 1997 measurements for these males. Thus, our sample size for this test was 58. The same data set was used to investigate the association

**Table 1**  
**Descriptive statistics for quality measures: body size (wing chord length), current physical condition (subcutaneous fat score on rank scale), territory size, prey abundance, and paternal care**

Measure	Mean	SD	n	Breast <sup>a</sup>		Rump <sup>a</sup>	
				$r_s$	<i>p</i>	$r_s$	<i>p</i>
Wing chord length (mm)	86.33	1.97	58	<b>.41</b>	.001*	<b>.41</b>	.002*
Subcutaneous fat score	1.55	1.36	55	-.12	.380	-.18	.200
Territory size (ha)	5.20	2.08	36	<b>.55</b>	.000*	<b>.49</b>	.002*
Prey abundance <sup>b</sup>	0.43	0.30	17	.11	.680	<b>.52</b>	.034
First-nest feeding rate (visits/h)	1.06	1.03	9	.32	.398	.66	.055
Later-nests feeding rate (visits/h)	0.28	0.35	15	.08	.776	.15	.590

<sup>a</sup> Spearman rank correlation coefficient ( $r_s$ ) calculated between each quality measure and male blueness score (composite of three plumage variables) on breast and rump body regions. Significant correlations (at  $\alpha = 0.05$ ) are in bold.

<sup>b</sup> Measured as mean wet weight of orthopterans, grams per 100-m transect per territory.

\* Correlation remains significant after a sequential Bonferroni correction for multiple comparisons (calculated separately for breast and rump).

between male blueness and fat score; however, three males were released before fat was measured, and thus sample size was 55 for this comparison.

Male body size as measured by wing chord length was significantly correlated with blueness score on both the breast and the rump region (Table 1 and Figure 3). To assess which components of the blueness score were driving this pattern, wing chord length was compared to each plumage variable separately (Table 2). On the breast, percent blue was positively correlated with wing chord length, and peak wavelength was negatively correlated with wing chord length as expected. On the rump, all plumage variables were significantly posi-

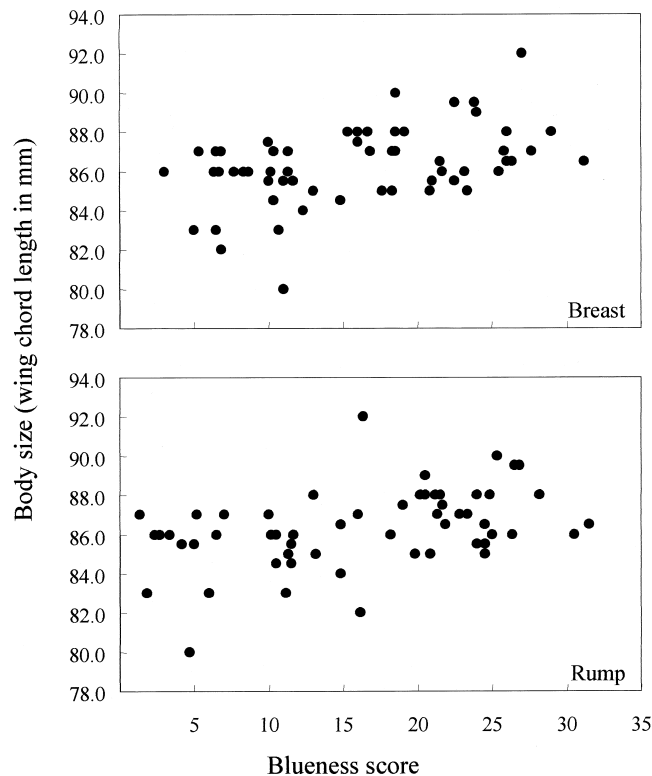
tively correlated with wing chord length with the exception of peak wavelength, which was significantly negatively correlated. Fat score, a measure of current physical condition, was not significantly associated with blueness. Feather lice load and avian pox measures proved to be nearly invariant in the population, and no analyses were performed.

**Territory size and quality**

During 1997 and 1998, 20 and 24 males, respectively, held breeding territories. Territories ranged in size from 0.80 ha to 8.73 ha. Seven of the 44 males bred in both years, and only 1997 data for these males were included in the analysis. An additional male was excluded from our analysis of the correlation between blueness and territory size due to lack of plumage data (thus,  $n = 36$ ). Territory size was strongly positively correlated with male blueness on both body regions (Table 1 and Figure 4). Separate analyses of the components of the blueness score showed that territory size was significantly correlated with percent blue on the breast but not on the rump region. Intensity was positively correlated with territory size, and peak wavelength was negatively correlated with territory size on both body regions (Table 2).

Prey abundance was successfully sampled within the territories of 17 males during 1998 (these data were not collected in 1997). A total of 198 samples were taken over an 8-week period, and each transect was sampled an average of 7.6 times. We calculated the average wet weight of orthopterans per 100-m transect within each male's territory over the course of the sampling period. This gave a single prey abundance value for each territory (i.e., available biomass measured as mean wet weight of orthopterans). Prey availability ranged from 0.16 g to 1.25 g per 100-m transect. Mean prey abundance per 100-m transect was compared to male plumage ornamentation ( $n = 17$ ). Orthopteran weight was significantly correlated with blueness on the rump but not with blueness on the breast (Table 1 and Figure 5). Further analyses revealed that percentage of blue feathers on the rump region is the only component of the blueness score associated with prey availability (Table 2).

Using logistic regression, we tested the hypothesis that male plumage blueness could signal the probability of nest predation in the territory (either increased or decreased risk). Thirty-six of the males were included in this analysis (same data set as used in territory size analyses). We monitored 76 nests and scored each based on successful fledging of young (1) or



**Figure 3**  
 Correlation between male blueness and body size measured as wing chord length (mm).

**Table 2**

Detailed analyses investigating correlation ( $r_s$ ) between four plumage variables and body size (wing chord length), territory size, prey abundance, and paternal care

Plumage variables	Breast				Rump							
	Wing chord length (mm) (58) <sup>a</sup>		Territory size (ha) (36)		Wing chord length (mm) (58)		Territory size (ha) (36)		Prey abundance <sup>b</sup> (17)		First-nest feeding rate (visits/h) (9)	
	$r_s$	$p$	$r_s$	$p$	$r_s$	$p$	$r_s$	$p$	$r_s$	$p$	$r_s$	$p$
Peak ( $\lambda$ )	<b>-.41</b>	.001*	<b>-.62</b>	.001*	<b>-.40</b>	.002*	<b>-.59</b>	.001*	-.33	.200	-.51	.162
Intensity	.05	.694	<b>.37</b>	.027	<b>.27</b>	.038	<b>.52</b>	.001*	.35	.168	.58	.104
Contrast	.03	.812	.28	.104	<b>.32</b>	.015	<b>.56</b>	.001*	.40	.117	.51	.162
% Blue	<b>.48</b>	.001*	<b>.41</b>	.013	<b>.36</b>	.005	.26	.131	<b>.54</b>	.025	.40	.289

Significant correlations (at  $\alpha = 0.05$ ) are in bold.

<sup>a</sup> Sample sizes in parentheses.

<sup>b</sup> Measured as mean wet weight of orthopterans, grams per 100-m transect per territory.

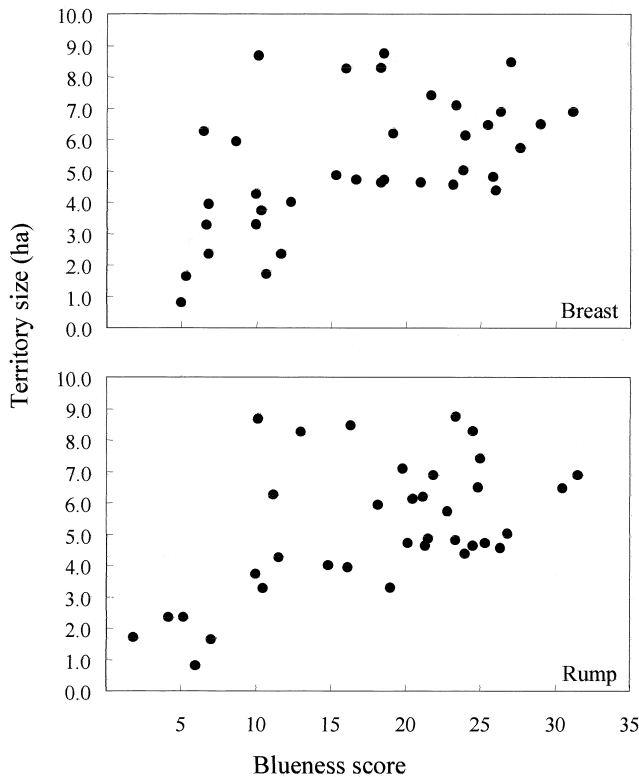
\* Correlation remains significant after a sequential Bonferroni correction for multiple comparisons (calculated separately for breast and rump).

failure due to predation (0). Abandoned nests or nests destroyed due to other causes (e.g., storms) were excluded. When we fit the logistic model in Equation 1 with blueness score on the breast as a predictor variable, there was no significant relationship between male ornamentation and risk of nest predation (test for significance of intercept and predictor variable:  $\chi^2 = 1.02$ ,  $p = .31$ ). When blueness score on the rump was the predictor variable, the results were also nonsignificant ( $\chi^2 = 0.03$ ,  $p = .87$ ).

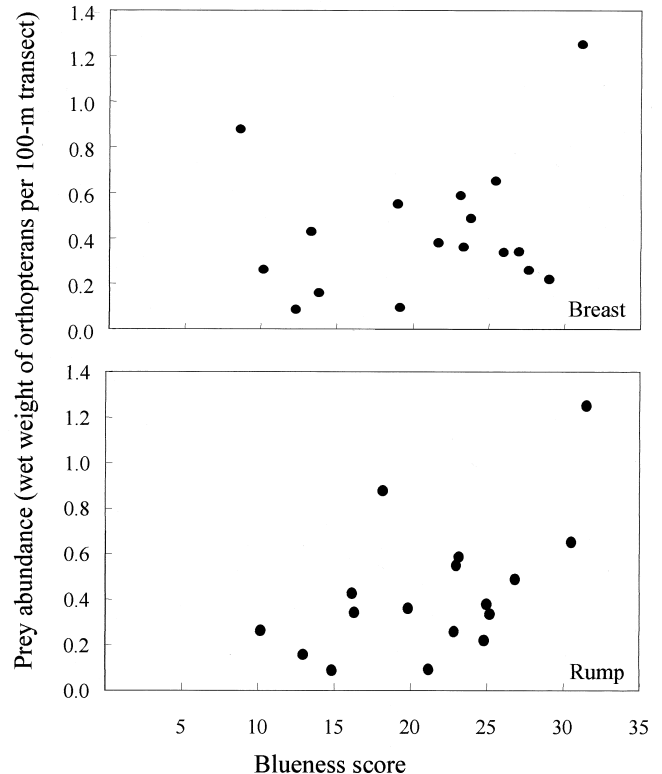
**Paternal investment**

On average, females fed nestlings at a rate more than six times higher than that of males (mean: 3.3 female feedings/h versus

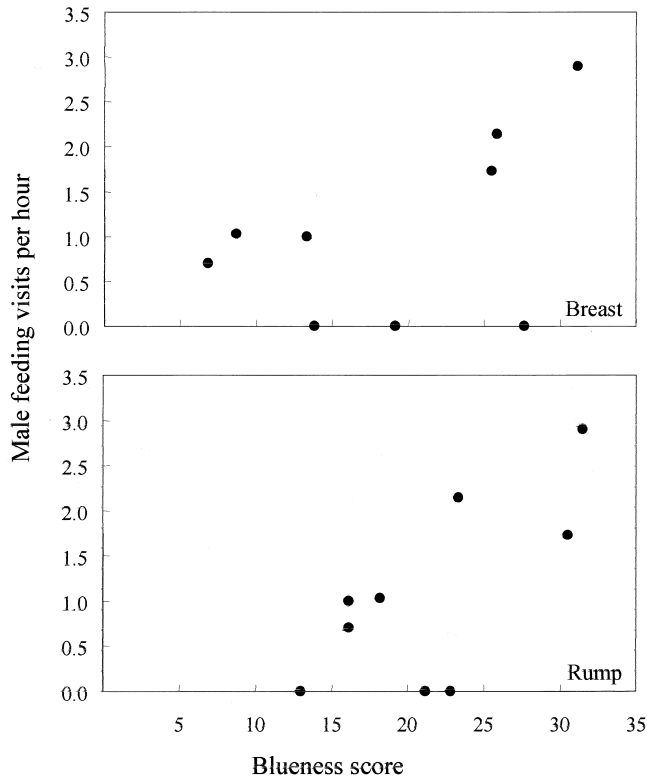
0.52 feedings/h for males). Male feeding rate was highly variable ranging from 0–2.9 feedings per hour. Male feeding rate did not vary with hour of the day (repeated-measures ANOVA,  $F = 0.665$ ,  $df = 13$ ,  $p = .798$ ) or with nestling age (repeated-measures ANOVA,  $F = 1.255$ ,  $df = 5$ ,  $p = .305$ ). However, male feeding rate appeared to be higher at the first nest of the season than at subsequent nests (repeated-measures ANOVA,  $F = 5.05$ ,  $df = 1$ ,  $p = .075$ ). For the analyses in this paper we pooled data over all hours of the day and all chick ages to calculate male feeding rate. However, we analyzed male feeding rate at first nests and feeding rate at later nests separately.



**Figure 4**  
Correlation between male blueness and territory size (ha).



**Figure 5**  
Correlation between male blueness and prey abundance (wet weight of orthopterans in grams per 100-m transect per territory).



**Figure 6**  
Correlation between male blueness and male feeding rate at the first nest of the season. There was no association between male blueness and male feeding visits at later nests.

When we compared male feeding rate at the first nest of the season to male blueness, we found a positive association between these two variables, as predicted (Table 1 and Figure 6), but this trend was nonsignificant for the breast ( $p = .398$ ) and only marginally significant for the rump ( $p = .055$ ). However, sample size was small for this analysis ( $n = 9$ ), and the near significance of the rump analysis suggests that there may be a pattern in the data. When male feeding rate at first nests was compared to each plumage variable separately, there were no statistically significant associations on the rump (Table 2). However, the near significance of the correlations between feeding rate and peak wavelength, intensity, and contrast suggested that all of these blueness components contributed to the correlation reported above. When male feeding rate at later nests was compared to blueness, there was no trend (Table 1).

## DISCUSSION

In this study, we found that extreme ornamentation in males, characterized by a high proportion of blue feathers in plumage and intense blue-ultraviolet coloration, was positively correlated with male body size, territory size, and prey abundance. The data also suggested that the bluest males may provide more parental care than less ornamented males; however, this result must be interpreted cautiously due to small sample size. These results are concordant with those of several studies investigating the function of pigment-based plumage ornaments. For example, in black-headed grosbeaks (*Pheucticus melanocephalus*), northern cardinals (*Cardinalis cardinalis*), and house sparrows (*Passer domesticus*), researchers found positive correlations between pigment-based ornaments and territory acquisition or social dominance (Hill, 1988; Møller,

1987; Veiga, 1993; Wolfenbarger, 1999). Positive correlations between paternal care of nestlings and male ornamentation have been documented in several avian species that display pigment-based ornaments (Hill, 1991; Norris, 1990; Sætre et al., 1995). There is also evidence that males displaying extreme plumage ornamentation obtain more extrapair matings than less ornamented males (Sundberg and Dixon, 1996; Yezzerinac and Weatherhead, 1997). Our observations of blue grosbeaks suggest that structurally based blue coloration may have the same sort of intraspecific signaling properties as pigment-based coloration, despite its different mechanistic basis.

The discovery of ultraviolet-sensitive retinal cones in birds (Chen and Goldsmith, 1986) sparked interest in the possible existence of hidden, ultraviolet signals in plumage (Bennett and Cuthill, 1994; Finger and Burkhardt, 1994). Researchers who tested for a role of ultraviolet color display in mate choice found that female starlings (*Sturnus vulgaris*) and zebra finches (*Taeniopygia guttata*) are sensitive to a lack of ultraviolet reflectance in male plumage (Bennett et al., 1996, 1997). The throat patch of male bluethroats (*Luscinia s. svecica*) has peak reflectance in the ultraviolet portion of the spectrum, and in aviary and field experiments, females discriminated against experimental males whose throat patch did not reflect ultraviolet light (Andersson and Amundsen, 1997; Johnsen et al., 1998). Moreover, in the field, male bluethroats with nonreflective throat patches guarded their mates more intensely, obtained fewer extrapair fertilizations, and were cuckolded more frequently than control males (Johnsen et al., 1998). In blue tits (*Parus caeruleus*), males and females, which appear nearly monomorphic to human observers, are dimorphic when ultraviolet plumage reflectance is measured (Andersson et al., 1998; Hunt et al., 1998). Females prefer males with the brightest ultraviolet ornaments (Hunt et al., 1998), and assortative mating based on ultraviolet coloration occurs in the wild (Andersson et al., 1998).

These studies demonstrate that ultraviolet coloration can be important in intraspecific interactions. Our previous work on blue grosbeaks demonstrated that males vary substantially in the wavelength of peak light reflectance and in the magnitude of reflectance in the ultraviolet portion of the spectrum (Keyser and Hill, 1999). Males did not vary randomly with respect to these two measures of color display. Rather, males with the greatest magnitude of light reflectance (most intensely colored males) also peaked at shorter wavelengths. Both the magnitude of maximum reflectance and wavelength of peak light reflectance were significantly positively correlated with nutritional condition during feather growth (Keyser and Hill, 1999). These findings set the stage for our current study, in which we showed that plumage blueness in male blue grosbeaks honestly advertises male quality.

Because expression of blue plumage depends on the physical condition of a male during the fall when new feathers are molted (Keyser and Hill, 1999), conspecifics assessing male ornamentation in the spring receive information about a male's past nutritional history. The correlation we found in this study between male plumage ornamentation and body size suggests that blueness may also provide information about the conditions in which a male was raised. The relationship between blueness and territory quality (and perhaps paternal care) documented here reflects the current status of a male. Thus, blue-ultraviolet plumage ornamentation is an honest advertisement of quality that can be assessed by conspecifics during mate choice or during male-male competition.

The question remains: does plumage blueness of male blue grosbeaks serve primarily as a signal between rival males, in female mate choice, or for both? Male body size was significantly positively associated with plumage blueness, but male size could be important in either female choice or male-male

competition. The strong association between territory size and male blueness, on the other hand, suggests an intrasexual function for male ornamentation because territory boundaries are established through direct male contests. It is interesting that all aspects of plumage blueness showed a significant association with territory size in the predicted direction, except percent blue on the rump. This may be due to reduced variance in percent blue on the rump (mean = 0.828,  $\sigma^2 = 0.062$ ) relative to the breast (mean = 0.694,  $\sigma^2 = 0.112$ ). Even birds whose plumage was almost 100% brown showed some proportion of blue feathers on the rump, which is often the bluest part of the body (Keyser and Hill, personal observations). Because the rump patch is often displayed during interactions with other males but rarely at any other time, rump coloration appears to function directly in male–male competition. Apparently, males prioritize development of blue rump feathers such that the rump is blue even when other parts of the plumage are brown, and this suggests that the rump plumage has a particularly important signaling function in male–male interactions.

The relationship between territory size and plumage blueness and the apparent directed display of colored plumage patches during male contests suggests that signaling between males may be a primary role for plumage blueness. However, the correlation between male ornamentation and prey abundance and paternal care indicates that female choice for highly ornamented males could be adaptive. Female mate choice has proven to be difficult to disentangle from male–male competition in territorial species (e.g., numerous red-winged blackbird studies summarized in Beletsky, 1996; Searcy and Yasukawa, 1995). If highly ornamented males establish and defend quality territories, then females may not need to assess males directly but instead may choose mates based on territory attributes. In this case, female choice and male ornamentation are indirectly linked, but it would be inaccurate to conclude that female choice was a selective pressure driving the evolution of male ornamentation. A more definitive assessment regarding the basis of mate choice in female blue grosbeaks will require controlled mate choice experiments.

A complementary approach to understanding female mate choice is genetic paternity analyses. One basic prediction of sexual selection theory is that more highly ornamented males should experience greater reproductive success than less ornamented males. It is now well established that in most species of birds some chicks are fathered outside the pair bond and that such extrapair paternity must be accounted for if success of individual males is to be accurately assessed (Birkhead and Møller, 1992; Gibbs et al., 1990; Weatherhead and Boag, 1995; Webster et al., 1995). In the indigo bunting (*Passerina cyanea*), a close relative of the blue grosbeak with a similar social system, 20–40% of offspring are fathered by males other than the attending male (Payne, 1992). Genetic paternity analyses of our marked blue grosbeak population are currently underway.

In general, males of many species are expected to experience higher variation in reproductive success than females. Thus competition among males for access to mates either through monopolization of resources or through exaggeration of traits that are attractive to females is expected (Darwin, 1871). From the female perspective, mate choice decisions can be costly in terms of time and energy. Female choice can be adaptive when it is based on male ornaments that provide honest information about male attributes (Searcy, 1979). The results of this study indicate that blue-ultraviolet coloration in blue grosbeaks is the kind of ornamental trait predicted by sexual selection theory (Kodric-Brown and Brown, 1984). The bluest males are also high-quality males. They are physically larger, hold larger territories with abundant prey, and con-

tribute to female provisioning at the nest. These results, in conjunction with other studies reviewed above, contribute to a more complete understanding of structurally based, ultraviolet plumage ornamentation in the context of sexual selection theory.

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