The Condor 115(4):902–909

PLUMAGE COLORATION OF THE BLUE GROSBEAK HAS NO DUAL FUNCTION: A TEST OF THE ARMAMENT–ORNAMENT MODEL OF SEXUAL SELECTION

Javier Quesada[1,3,4,5], Carlos Alberto Chávez-Zichinelli[2,4], Juan Carlos Senar[3], and Jorge Ernesto Schondube[4]

[1]*Catalan Ornithological Institute, Natural History Museum of Barcelona, Barcelona, Spain*
[2]*Universidad Autónoma de Tlaxcala, Centro Tlaxcala de Biología de la Conducta, Tlaxcala, Mexico*
[3]*Evolutionary and Behavioral Ecology Associate Research Unit, Consejo Superior de Investigaciones Científicas, Natural History Museum of Barcelona, Barcelona, Spain*
[4]*Laboratorio de Ecología Funcional, Centro de Investigaciones en Ecosistemas, Universidad Nacional Autónoma de México, Morelia, Mexico*

Abstract. Although plumage coloration has been widely used as a model in studies of the evolution of signaling, the role of plumage in intrasexual communication has been less studied, especially in cases of the structural plumage color. The aim of our study was to use choice trials and plumage manipulation to test whether or not the structural blue color of the male Blue Grosbeak (*Passerina caerulea*) works as a signal of social status. Additionally, we tested whether or not females exploit signals used in aggression between males. If they do, it suggests that plumage coloration is also used in mate choice. In 2007, we captured males and females from two different populations. We performed two choice experiments by manipulating plumage color: (1) a status-signaling experiment, in which a male had to choose one of two other males, and (2) a mate-choice experiment, in which a female had to choose one of two males. Males clearly foraged near less blue birds during their first encounter and on the first day. However, this preference was not evident on subsequent days. Females showed no preference for any color of male. Our data show that plumage color works as a "first impression" signal, which suggests that plumage coloration in the Blue Grosbeak represents a signal of dominance status between unfamiliar individuals and thus supports the status-signaling hypothesis. Our results support previous evidence for a lack of selection of males by females, which for this species thus rebuts the armament–ornament model of sexual selection.

Key words: *armament–ornament model, Blue Grosbeak, male–male competition, mate choice,* Passerina caerulea*, status-signaling hypothesis, structural plumage color.*

La Coloración de Plumaje del *Passerina caerulea* no Tiene una Función Dual: Un Test del Modelo Armamentos–Ornamentos de la Selección Sexual

Resumen. La coloración del plumaje ha sido ampliamente utilizada como modelo de estudio para comprender la evolución de la señalización. Sin embargo, pocos estudios han analizado el papel que tiene la coloración estructural del plumaje dentro de la comunicación intra-sexual. El objetivo de este estudio fue analizar si la coloración estructural del plumaje funciona como una señal de estatus social a través de experimentos de selección en los que se manipuló la coloración de plumaje de machos de *Passerina caerulea*. Adicionalmente, se analizó si las hembras explotaban esta señal de agresión entre machos. Si esto último fuera así, sugeriría que la coloración del plumaje se utiliza también para escoger pareja. En 2007, se capturaron machos y hembras de dos poblaciones diferentes de *P. caerulea*. Se realizaron dos experimentos de selección mediante la manipulación del color del plumaje de los machos: (1) un experimento de señalización de estatus, el cual consistió en que un macho seleccionara a uno de otros dos machos para forrajear y (2) un experimento de selección de pareja, en el cual una hembra tuviera que elegir entre dos machos. Los resultados mostraron que los machos preferían forrajear con aquellos otros machos cuya coloración del plumaje era menos azul durante su primer encuentro y durante el primer día del experimento. Sin embargo, esta preferencia no fue evidente al segundo día. Las hembras, no obstante, no mostraron preferencia alguna por ninguno de los dos machos manipulados. Nuestros resultados muestran que la coloración estructural del plumaje puede funcionar como una señal de "primera impresión", lo que indica que la coloración del plumaje del *P. caerulea* funciona como una señal de estatus entre individuos que no se conocen, apoyando así la hipótesis de señalización de estatus. Nuestros resultados también apoyan evidencias previas de una falta de selección de los machos por parte de las hembras, lo cual refuta el modelo de ornamentos-armamentos para esta especie.

Manuscript received 19 January 2012; accepted 8 May 2013.
[5]Current address: Natural History Museum of Barcelona, Chordates Laboratory, Passeig Picasso s/n, 08003 Barcelona, Spain.
E-mail: jquesadal@bcn.cat

The Condor, Vol. 115, Number 4, pages 902–909. ISSN 0010-5422, electronic ISSN 1938-5129. DOI: 10.1525/cond.2013.120009

INTRODUCTION

Plumage coloration has been used widely as a model in the study of the evolution of signaling behavior (Andersson 1994, Møller 1994, Hill and McGraw 2006b). The study of both structural and pigment-based colors has provided many insights that support the idea that these traits are used as honest signals of the qualities of the bearer in terms of parental care, parasites, or body condition (Andersson 1994, Møller 1994). Structural plumage color is created by light reflected by the microstructures of the feathers, which consist essentially of a combination of a keratin matrix with melanocytes and air vacuoles embedded within it (Prum 2006). In pigmented feathers, on the other hand, pigments are embedded in this matrix or form a layer within the matrix, and it is this combination of pigments and the structural matrix that gives feathers their final apparent color (Prum 2006).

Plumage color is used both during mate choice (Hill and McGraw 2006a, Hill and McGraw 2006b) and as a signal of dominance in aggressive interactions (Senar 2006). According to the armament–ornament model (Berglund et al. 1996), females may exploit signals used in contests of aggression between males to improve their mate choice. Consequently, status signals may have a dual function and play a part in both intra- and intersexual signaling. This dual function has been described previously for melanin- and carotenoid-based plumage colors (Griggio et al. 2007, Hoi and Griggio 2008), although there are cases for which this dual function does not hold (Senar 2006). Nevertheless, no dual function has ever been described in the case of structural-based color traits. Some studies have reported that these traits may be used as indicators of dominance and fighting ability (Alonso-Alvarez et al. 2004, Rémy et al. 2010, Siefferman and Hill 2005a, but see Vedder et al. 2008) and UV manipulation has shown that some of these traits have an important role in females' mate choice (Bennett et al. 1997, Hunt et al. 1999, Keyser and Hill 1999, Siefferman and Hill 2005b). However, very few studies have simultaneously tested within the same species the effects of structural plumage coloration in both male–male competition and females' mate choice. The first aim of our study was therefore to test the armament–ornament model for structural coloration (Berglund et al. 1996) by analyzing the role of the blue plumage in the Blue Grosbeak (*Passerina caerulea*) in both social-status signaling and mate choice.

The blue structural color of the Blue Grosbeak has been the object of much study in the past (Keyser and Hill 1999, 2000, Ballentine and Hill 2003). This trait is sexually dimorphic, adult males being blue with some brown spots and the females completely brown (Pyle et al. 1987). Previous work has shown significant variation in the blue of the males. The blue of the Blue Grosbeak reflects in the UV range and has been shown to be an honest indicator of body condition and to be positively related to territory size and quality (Keyser and Hill 1999, Keyser and Hill 2000). The status-signaling hypothesis was posited by Rohwer (1975) and states that certain plumage patches serve as signals of social status and thereby provide information regarding the resource-holding potential or aggressiveness of their bearer (Senar 2006, Vedder et al. 2010).

Originally, this principle was thought to only to species in which individuals interact with many other competitors or between unknown rivals; indeed, this was one of the key assumptions of this hypothesis (Senar 2006). Surprisingly, experimental evidence on the subject is very scarce (Lemel 1993, Brotons 1998, Vedder et al. 2010), and no experiments have been designed specifically to tackle this question (Senar 2006, but see Vedder et al. 2010). If status signals serve as a first impression an experiment should therefore be designed in which unknown birds do not interact physically—to be able to test the reliability of the signal—and in which the "efficiency" of the status signal is negatively related to the number of interactions (Senar 2006).

The second aim of our study was to test whether the blue structural color of the Blue Grosbeak works as a "first impression" signal of social status. If this is the case, a male having to choose between feeding with an apparently dominant or a subordinate flock companion (a "choice test") (Senar and Camerino 1998, Senar 2006) will initially avoid the dominant male but over time this avoidance will diminish.

MATERIAL AND METHODS

GENERAL PROCEDURES

In 2007, we captured adult male and female Blue Grosbeaks at the beginning of their breeding season (March–May) at two localities in the state of Michoacan, western Mexico. The first locality was the campus of the Universidad Nacional Autónoma de México in Morelia, a suburban habitat with buildings, *Eucalyptus* spp., and many native grasses and shrubs. The second locality was in shrubland near the town of Chiquimitio, 50 km away. All birds were handled during capture and in the laboratory according to the *Guidelines for the Use of Wild Birds in Research* (Gaunt et al. 1999).

Birds were mist-netted, banded, sexed, measured (tarsus and wing), and weighed. We ensured that all birds taken into captivity lacked any reproductive characteristics (brood patches in females or cloacal protuberances in males) to avoid experiments on birds that were actively nesting. We also took digital pictures in a standardized position of birds laid on their backs on a grid of 1 × 1 mm placed next to a reference guide to colors (Figuerola and Senar 2000). After the pictures were taken, we plucked 15–20 breast and rump feathers from each bird for further spectrophotometric analysis (Quesada and Senar 2006).

All birds were individually housed in cages of 1 × 0.90 × 1 m with the sides and backs covered so that there was no visual contact between them (although they could hear each other). All cages contained two long wooden perches, a feeder, and a water bottle. They had good ventilation and were illuminated by natural light from a large window. The size of the cages allowed the birds their normal activities and to flap their wings (Gaunt et al. 1999). The birds were given water ad libitum and a diet of mixed grains supplemented with a vitamin complex. All birds suffered a degree of stress when first captured and lost some mass. For this reason, we did not start the experiments until they had regained their original mass (within approximately two weeks). In addition, to minimize stress in captivity, we cleaned their cages and provided food and water in darkness.

ANALYSIS OF PLUMAGE COLORATION

To assess plumage coloration, we layered the plucked breast feathers on black velvet (reflectance 0%) in an arrangement that replicated the natural arrangement on the bird (Quesada and Senar 2006). We used a USB2000 spectrometer connected to a computer with the program SpectraSuite and a DT-MINI140 GWS deuterium tungsten halogen light source (220–2000 nm) (Ocean Optics, Duiven, the Netherlands). We measured all spectra with reference to a white substance (WS-1, Diffuse Reflectance Standard) with a reflectivity of over 98% and a dark spectrum (spectrum taken with the lamp blocked to correct for contamination by ambient light). We took three measurements per sample, then computed the mean. We considered a tri-stimulus perspective by using three measurements of color (brightness, chroma, and hue). Brightness corresponds to the physical intensity of light reflected from a surface. Chroma (also called saturation or intensity) is positively correlated with a color's monochromatism or purity. Hue corresponds to the color's main wavelength (red, orange, green, etc.) (Minolta Company 1994, Fairchild 2005). Hence we computed, the coloration variables as follows: for each spectrum, we assessed brightness as the mean value of reflectance for the whole spectrum (Andersson et al. 1998, Doucet and Montgomerie 2003), we calculated the chroma as the proportion of reflectance from the UV (300–400) region in relation to the total reflectance of the spectrum (300–700 nm) (Andersson et al. 1998), and we considered hue as the wavelength with the greatest reflectance (Andersson et al. 1998, Keyser and Hill 1999, Doucet and Montgomerie 2003).

The Blue Grosbeak often has brown spots within its mainly blue plumage that may act as a confounding variable, so these spots have to be standardized. To do so, we evaluated the "spottiness" of each bird from the digital pictures taken in the field before the bird was taken into captivity. We drew three straight lines perpendicular to the bird's longitudinal axis under its chin, across the middle of its breast, and 1 cm above its cloaca. We assessed the percentage of brown along these lines in relation to the whole line and computed the mean of the three lines.

GENERAL EXPERIMENTAL SETUP

The tests of status signaling (male–male interaction) and mate choice (female–male interaction) consisted of the release of an experimental bird into a cage (2 × 0.5 × 0.5 m; Fig. 1a) in which it had to associate with one of two males each in a smaller cage (both 0.25 × 0.25 × 0.35 m) located at either end of the larger cage (Fig. 1b). As in the experiment of Ballentine and Hill (2003), we colored the plumage of the males in the smaller cages completely with a nontoxic black Sharpie marker (Newell Rubbermaid, Oak Brook, IL) or blue Tria marker (Letraset Ltd., Ashford, England) marker. Thus the plumage of one of the two males was artificially dulled (the "darkened" bird), that of the other enhanced (the "blue" bird). In this way, we were able to manipulate a bird's single UV peak in a natural way and ensure that chroma and brightness were changed while hue was unaffected (Ballentine and Hill 2003).

The two cages that housed the manipulated birds consisted of fish tanks placed on an expanded polystyrene base. The fish tanks were inverted and fitted into a groove previously made in the base. Thus the cages were soundproofed so that the experimental bird was unable to use acoustic cues to select between the manipulated birds. We inserted

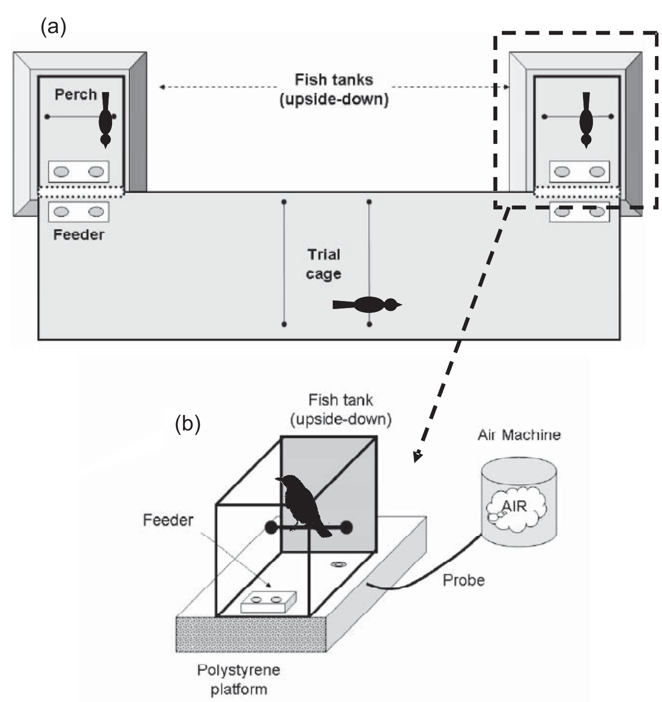

FIGURE 1. Experiment design of the test of choice of the Blue Grosbeak for a blue or a darkened male.

in the base of the expanded polystyrene a probe connected to a silenced ventilator to provide air. All the walls of the fish tanks were covered except for the side facing the experimental cage, on which a feeder was placed (Fig. 1b). All trials were recorded on a laptop computer with a camera, which was placed in front of the cage of the experimental bird. At the end of the experiment, we analyzed the recordings. To avoid observation bias, the video recordings were analyzed by an observer with no knowledge of how the manipulations had been carried out (CACZ).

Although we controlled for several confounding variables, it could be argued that other variables besides song and display—for example, spottiness, tarsus size, weight, or the original plumage coloration of the two manipulated birds—were not controlled for in our experiment and could have affected our results. However, all differences between the darkened and blue bird in each dyad did not differ from 0 (*t*-test for single means, Table 1) in either the male–male or the male–female selection trials.

MALE–MALE SELECTION TRIALS

The status-signaling trials consisted of the release of a male, the "experimental bird," into the large cage so that he could feed in front of one or other of the two manipulated birds (the "darkened" or the "blue" bird). We also placed two perches in the middle of the experimental cage to allow the experimental bird to not interact with either of the manipulated birds (Fig. 1a). We located two feeders in front of the fish tanks so that when feeding the experimental bird would come face to face with one or the other of the bird feeders in the cages housing the manipulated birds (Fig. 1a). The trials took place in the morning (07:00–11:00) in a large soundproofed room with polarized natural light to ensure that the reflections from the glass did not affect the experiment. The room's windows were located to the sides and behind the fish tank. We performed 20 male–male trials, although we discounted the results of one as one of the birds damaged a wing during the experiment.

The experiment as a whole consisted of a control and then trial experiments. The trial experiments had three stages that allowed us, first, to determine whether or not the experimental bird preferred one or the other of the manipulated birds and, second, to evaluate whether or not plumage works as a "first impression" or as a "constant" signal. On the first day we evaluated the choice of the experimental bird during the first 5 min of interaction (stage 1), then continued the evaluation for 2 hr (stage 2); finally, we observed the bird's behavior for a further 2 hr the next day (stage 3).

During the control test, the experimental bird was left for 2 hr in the cage to allow it to familiarize itself with its surroundings prior to the experiment. We did not provide any food until the second hour in order to evaluate its possible preference for one side or the other of the cage. Then, without removing the experimental bird from the cage, we placed the manipulated birds in the fish tanks, ensuring that they had no physical or acoustic contact with the experimental bird. We assigned the manipulated birds randomly to one or the other fish tank. All birds (experimental and manipulated) spent the night in the cages. The next day, we carried out the trial experiment with the manipulated birds. First, we left all birds without food for 2 hr, then provided food. We allowed the experimental bird to have visual contact with the two manipulated birds for 2 hr. We repeated the same protocol with the manipulated birds on the second day.

FEMALE–MALE SELECTION TRIALS

For mate-choice trials (n = 11), we used the same protocol as for status-signaling trials (control experiment and two experimental days with the manipulated males). In this case, however, the experimental bird was a female and we used a perch on either side of the cage instead of feeders. In this way, the absence of feeders in the experimental cage enabled us to evaluate the female's preference for a male rather than her preference for eating close to another bird. Thus there were only four perches, two in the center of the cage and two in front of the fish tanks occupied by the manipulated birds.

For both experiments, we used 20 males and 11 females. Each bird performed once in the status-signaling trials as an

TABLE 1. Differences in biometry and plumage coloration between pairs of manipulated birds used in each trial for both male–male and male–female interactions. We used a *t*-test to assess whether the difference between the darkened bird and blue bird was significantly different from 0. No difference was significant, which indicates that these variables were chosen at random.

	In male–male trials				In male–female trials			
Trait	Mean	SE	t_{18}	P	Mean	SE	t_{10}	P
Spottiness (%)	1.7	1.22	1.39	0.18	–0.77	1.81	–0.43	0.68
Tarsus (mm)	–1.26	1.1	–1.14	0.27	0.09	0.22	0.41	0.69
Weight (g)	–1.82	1.54	–1.18	0.25	0.04	0.73	0.05	0.96
Brightness (%)	0.36	0.34	1.05	0.31	–0.26	1.64	–0.16	0.88
Chroma (%)	0.09	0.07	1.29	0.21	–1.7	4.08	–0.42	0.69
Hue (nm)	–1.84	2.71	–0.68	0.51	–4	2.76	–1.45	0.18

experimental bird and twice as a manipulated bird. We used each bird several times but avoided using the same three birds together in more than one trial; thus all trials were always conducted with a set of birds that were unknown to each other.

Once the experiments were finished, we released the birds at the sites of their original capture after they completed their molts in the cages. In this way we assured that no evidence of plumage manipulation remained. Throughout the experiments, all released birds maintained a constant body mass which was similar to their original weight when first captured.

STATISTICAL ANALYSES

To evaluate social preferences, we carried out a Wilcoxon's signed-rank test for matched pairs between the percentages of time spent with the blue or the darkened bird in each stage of the experiment. We first evaluated the "first impression" as the preference for the darkened or the blue bird within the first 5 min. Then we evaluated experimental bird's preferences after 90 min ("day 1") and then again for 90 min on the second day ("day 2"). We analyzed the sexual preferences of females in the same way and used Statistica 7.0 for all statistical analyses. We set the level of significance at $\alpha = 0.05$, and the values reported under Results are means ± SE or medians ± 25 and 75% quartiles (depending on the analysis used).

RESULTS

MALE-TO-MALE TRIALS

Our control experiment showed that, as expected, experimental males showed no preference for either side of the cage (Table 2). On the other hand, experimental birds clearly preferred feeding beside the darkened bird during the first impression and during day 1 (Fig. 2, Table 2). But this tendency was no longer significant on day 2 (Table 2). Hence these results reveal that test males avoided the blue birds and preferred eating alongside the darkened birds.

INTERSEXUAL TRIALS

Females showed no preference for either the darkened or the blue bird, either during the first impression or during the 2-hr trials on either day 1 or day 2 (Table 2).

DISCUSSION

The role of structural color has received a great deal of attention in recent years. Several studies have demonstrated that manipulation of UV color affects the behavior of both sexes toward conspecifics and that UV structural color may play an important role in signaling an individual's qualities (Bennett et al. 1997, Andersson and Amundsen 1997, Hunt et al. 1998, Sheldon et al. 1999, Siitari et al. 2002, Alonso-Alvarez et al. 2004, but see Vedder et al. 2010). Although useful for understanding the role of structural color in sexual or social-status signaling, many of the plumage modifications used in these studies unfortunately consisted of unnatural alterations in plumage color (Ballentine and Hill 2003). Thus it is difficult to decide whether the observed effect was due to the subject's responding naturally to a "poor-quality" male or to a "bizarre" bird (Ballentine and Hill 2003). For this reason, we sought to manipulate birds in a more realistic fashion.

In our study, we followed the same procedure used by Ballentine and Hill (2003) but also controlled for confounding variables such as spottiness, the male's song (birds were kept in sound-proofed cages), and flight displays (manipulated birds were kept in cages too small to allow them to display). We found that male Blue Grosbeaks preferred to eat beside darkened male birds, which suggests that in this species plumage signals social status. This result coincides with recent studies that assign a social role to structural color (Alonso-Alvarez et al. 2004, Siefferman and Hill 2005a, Rémy et al. 2010). Our results also agree with previous studies of the Blue Grosbeak associating structural color with dominance. Keyser and Hill (2000) found more brightly

TABLE 2. Results of the Wilcoxon signed-rank tests for matched pairs in the social and sexual selection experiments measured as the percentage of time spent with a "blue" or "darkened" manipulated birds.

	% time visiting "blue" bird		% time visiting "darkened" bird				
	Median	25–75% quartile	Median	25–75% quartile	*n*	*W*	*P*
Male–male trials							
Control[a]	59.07	32.83–98.76	40.93	1.24-67.17	16	45	0.25
5 min	0	0.00–0.00	100.00	100.00–100.00	15	24	0.02
Day 1	10.28	0.00–64.12	89.73	35.88–100.00	19	30	0.005
Day 2	53.26	30.43–85.59	46.75	14.41–69.57	13	32	0.35
Female–male trials							
Control[a]	100	0.00–100.00	0.00	0.00–100.00	6	7	0.30
5 min	50	0.00–100.00	50	0.00–100.00	10	27.5	0.98
Day 1	6.97	4.10–87.52	93.03	12.48–95.90	11	21	0.30
Day 2	53.89	15.26–84.53	46.11	15.47–84.74	11	29	0.77

[a]In control trials the choice was not between two birds but between two feeders at the empty right and left ends of the experimental setup.

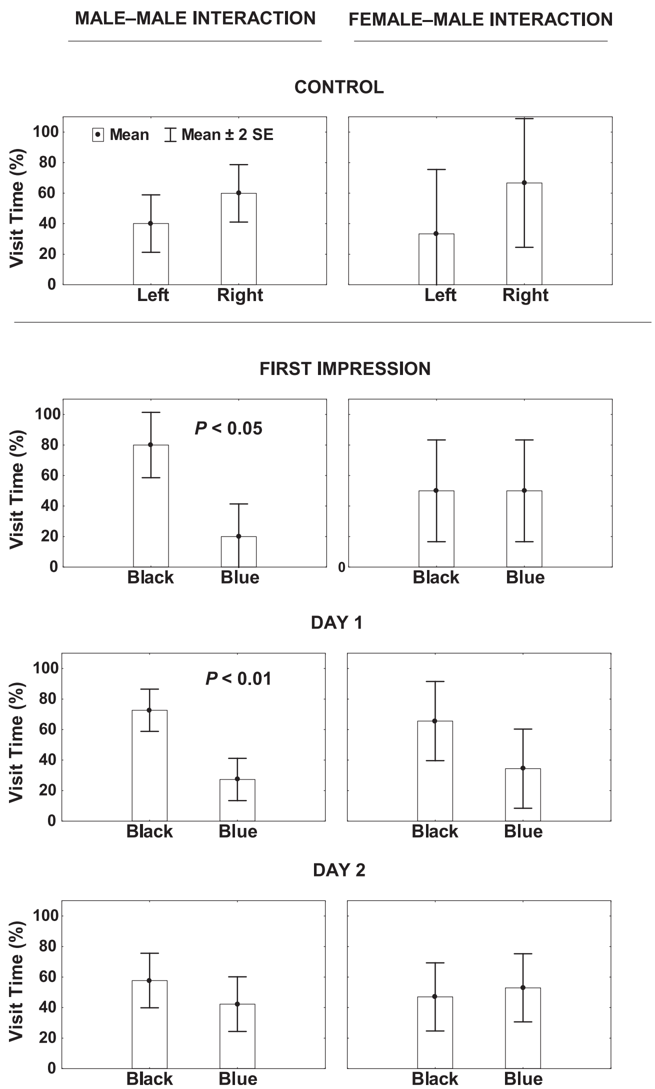

FIGURE 2. Differences in the percentage of time an experimental Blue Grosbeak spent with a "blue" or "darkened" manipulated male in the status-signaling trials. The choice experiment consisted of three stages: an evaluation of the first impression of the experimental bird during the first 5 min of interaction, an evaluation during the following 2 hr (day 1), and an evaluation on the second day consisting of the observation of the bird's behavior for 2 more hr.

colored birds to be in better body condition and hold better territories. The quality of a male's territory or its body condition frequently depends on its dominance status (Beletsky and Orians 1989, Piper and Wiley 1990, Smith 1994, Hake 1996, Gosler and Carruthers 1999, Hogstad 1999, Senar et al. 2000).

However, although our study shows that the blue plumage of the Blue Grosbeak works as a signal of social status, we were unable to confirm whether or not the behavior or bluer birds reflects higher status, as in greater aggressiveness or subjective resource motivation (the "perceived value" of a resource contested by two competitors), or whether bluer plumage is related to its wearer's potential to hold resources (Vedder et al. 2010). Hence further research is needed to discriminate between these different components of dominance.

THE ROLE OF STRUCTURAL PLUMAGE COLOR IN MATE CHOICE IN THE BLUE GROSBEAK

It is widely accepted that in birds bright colors can be explained largely by sexual selection, which may work via mechanisms of mate choice or of male–male interaction. In the latter case, females exploit signals of status as an honest cue for assessing a male's quality. Hence, a signal of social status may have evolved from selective pressures, sexual selection (mediated by mate choice), or natural selection (mediated by male–male interaction). This duality has been shown to exist in some passerines (see Griggio 2007, Hoi and Griggio 2008) but not in others (Senar et al. 2005, Liu et al. 2007). Our results support previous evidence for a lack of direct selection of males by females in the Blue Grosbeak (Ballentine and Hill 2003) and in other species with structural color (Liu et al. 2007) or in those with only pigment-based colors (Senar et al. 2005). Females may pay more attention to a male's ability to acquire other resources that could be related to plumage coloration or dominance status. For example, a dominant male may signal his fighting ability to other males in order to acquire a better territory and so females will use territory quality to choose their mates. Nevertheless, males could use other signals (song, display, etc.) that we did not consider in our study. For instance, we modified brightness and chroma, but did not manipulate any other color-related variable such as hue, for which females may also be select. More studies are still needed to explore these considerations, above all given the evidence suggesting that different features of the same plumage may signal different qualities (Doucet and Montgomerie 2003, Ferns and Hinsley 2008, Senar et al. 2008).

Senar (2006) reviewed a third way in which selection pressure could explain bright colors in birds. Dominance-related traits such as plumage color may evolve through social interaction without giving any advantage in mate choice. For example, in the European Siskin (*Spinus spinus*) the male's black bib is a useful signal in winter interactions between males but is not used by females as a trait for choosing a mate in the breeding season (Senar et al. 1998, Senar 2006). In the Blue Grosbeak, we cannot rule out the potential role of sexual selection in explaining the evolution of plumage color given that previous studies have found that brighter males have better territories (Keyser and Hill 2000); nevertheless, it seems clear that females do not use this character directly when assessing males.

STRUCTURAL PLUMAGE COLOR AS A "FIRST IMPRESSION" TRAIT

An interesting finding was that plumage color worked as a "first impression" signal. Many studies have discussed whether or not dominance signals work indefinitely as a clue to fighting abilities or only as a "first impression" signal (Senar 2006), thereby supporting the premises underlying the status-signaling hypothesis (Rohwer 1975, 1982). When two birds that do not know each other come into conflict, their first evaluation is visual, that is, birds will use "cues" (such as status signals, size, etc.) to assess the status of the opponent (its aggressiveness or resource-holding potential). Once the bird has experience with its competitor, other factors (e.g., subjective motivation, personality, or experience) may diminish the signaling value of the colored patch (see Vedder et al. 2010). Hence we can expect that the effect of the signal will diminish the longer the birds interact. Our results support this view, as we found that there was a strong effect of avoiding the blue bird on the first day of the test but no such relationship on the second day. This finding suggests that the Blue Grosbeak's blue plumage is a trait that signals dominance when unfamiliar individuals meet and hence provides support for one of the main (but rarely tested) assumptions of the status-signaling hypothesis. However, it is likely that birds probably use a number of other cues to evaluate the true fighting abilities of a competitor (Bókony et al. 2006).

On day 2 of the experiment we expected the effect to diminish but not so abruptly to insignificance. Although our results would seem to be proof that the signal worked as a "first impression," it could instead be an experimental artifact linked to the way in which birds become accustomed to the presence of harmless rivals. Thus, although the experimental males recognized that the other more brightly colored males were dominant, the former eventually lost their fear of being attacked by the dominant male when no aggressive behavior was forthcoming. In summary, our experiment showed that structural color in the Blue Grosbeak works as a signal of social status between unfamiliar competitors, thereby supporting the status-signaling hypothesis. However, females do not seem to use this trait in mate choice. Consequently, the blue plumage of the Blue Grosbeak does seem not to have a dual function, refuting for this species the armament–ornament model of sexual selection (Berglund et al. 1996).

ACKNOWLEDGMENTS

We thank everybody at the Functional Ecology laboratory for their help and support during this study, above all, Lorena Pérez Morales. Sr. Agustin kindly allowed us to carry out the field work on his property in Chiquimitio. Two anonymous referees made useful comments on an earlier version of the manuscript. Michael Lockwood kindly revised the English. This study was funded by a postdoctoral grant from the Centro de Investigaciones en Ecosistemas to JQ, scholarship 48612 from the Consejo Nacional de Ciencia y Tecnología (CONACYT) to CACZ, projects SDEI–PTID–02 and IN228007-3 of the Programa de Apoyo a Proyectos de Investigación e Innovación Tecnológica, and projects 65503 (JES) and CGL 2012-38262 (JCS) of CONACYT and the state government of Michoacan. Our research protocols were authorized by permit FAUT-0193 from the Oficina de Fauna Silvestre, Mexico, to JES and approved by the animal-care and -use committee of the Universidad Nacional Autónoma de México.

LITERATURE CITED

Alonso-Alvarez, C., Doutrelant, C., and G. Sorci. 2004. Ultraviolet reflectance affects male–male interactions in the Blue Tit (*Parus caeruleus ultramarinus*). Behavioral Ecology 15: 805–809.

Andersson, M. 1994. Sexual selection. Princeton University Press, Princeton, NJ.

Andersson, S., and T. Amundsen. 1997. Ultraviolet colour vision and ornamentation in Bluethroats. Proceedings of the Royal Society of London B 264:1587–1591.

Andersson, S., J. Ornborg, and M. Andersson. 1998. Ultraviolet sexual dimorphism and assortative mating in Blue Tits. Proceedings of the Royal Society of London B 265:445–450.

Ballentine, B., and G. E. Hill. 2003. Female mate choice in relation to structural plumage colouration in Blue Grosbeaks. Condor 105:593–598.

Beletsky, L. D., and G. H. Orians. 1989. Territoriality among male Red-winged Blackbirds.3. Testing hypotheses of territorial dominance. Behavioral Ecology and Sociobiology 24:333–339.

Bennett, A. T. D., I. C. Cuthill, J. C., Partridge, and K. Lunau. 1997. Ultraviolet plumage colors predict mate preferences in starlings. Proceeding of the National Academy of Sciences of the USA 94: 8618–8621.

Berglund, A., A. Bisazza, and A. Pilastro. 1996. Armaments and ornaments: an evolutionary explanation of traits of dual utility. Biological Journal of the Linnean Society 58:385–399.

Bókony, V., A. Z. Lendvai, and A. Liker. 2006. Multiple cues in status signalling: the role of wingbars in aggressive interactions of male House Sparrows. Ethology 112:947–954.

Brotons, L. 1998. Status signalling in the Coal Tit (*Parus ater*): the role of previous knowledge of individuals. Etología 6:49–52.

Doucet, S. M., and R. Montgomerie. 2003. Multiple sexual ornaments in Satin Bowerbirds: ultraviolet plumage and bowers signal different aspects of male quality. Behavioral Ecology 14:503–509.

Fairchild, M. D. 2005. Color appearance models, Wiley, Chichester, England.

Ferns, P. N., and S. A. Hinsley. 2008. Carotenoid plumage hue and chroma signal different aspects of individual and habitat quality in tits. Ibis 150: 52–159.

Figuerola, J., and J. C. Senar. 2000. Measurement of plumage badges: an evaluation of methods used in the Great Tit *Parus major*. Ibis 142:482–484.

Gaunt, A. S., L. W. Oring, K. P. Able, D. W. Anderson, L. F. Baptista, J. C. Barlow, and J. C. Wingfield. 1999. Guidelines for the use of wild birds in research, 2nd edition. Ornithological Council, Washington, DC.

Gosler, A., and T. Carruthers. 1999. Body reserves and social dominance in the Great Tit (*Parus major*) in relation to winter weather in southwest Ireland. Journal of Avian Biology 30:447–459.

Griggio, M., L. Serra, D. Licheri, A. Monti, and A. Pilastro. 2007. Armaments and ornaments in the Rock Sparrow: a possible dual utility of a carotenoid-based feather signal. Behavioral Ecology and Sociobiology 61:423–433.

Hake, M. 1996. Fattening strategies in dominance-structured Greenfinch (*Carduelis chloris*) flocks in winter. Behavioral Ecology and Sociobiology 39:71–76.

Hill, G. E., and K. J. McGraw [eds.]. 2006a. Bird coloration, volume 2: function and evolution. Harvard University Press, Cambridge, MA.

Hill, G. E., and K. J. McGraw [eds.]. 2006b. Bird coloration, volume 1: mechanisms and measurements. Harvard University Press, Cambridge, MA.

Hogstad, O., 1999. Territory acquisition during winter by juvenile Willow Tits (*Parus montanus*). Ibis 141:615–620.

Hoi, H., and M. Griggio. 2008. Dual utility of a melanin-based ornament in Bearded Tits. Ethology 114:1094–1100.

Hunt, S., A. T. D. Bennett, I. C. Cuthill, and R. Griffiths. 1998. Blue Tits are ultraviolet tits. Proceedings of the Royal Society of London B 265:451–455.

Hunt, S., I. C. Cuthill, A. T. D. Bennett, and R. Griffiths.1999. Preferences for ultraviolet partners in the Blue Tit. Animal Behaviour 58:809–815.

Keyser, A. J., and G. E. Hill. 1999. Condition-dependent variation in the blue-ultraviolet colouration of a structurally based plumage ornament. Proceedings of the Royal Society of London B 266:771–777.

Keyser, A. J., and G. E. Hill. 2000. Structurally based plumage colouration is an honest signal of quality in male Blue Grosbeaks. Behavioral Ecology 10:202–209.

Lemel, J. 1993. Evolutionary and ecological perspectives of status signalling in the Great Tit (*Parus major* L.). Ph.D. dissertation, Göteborg University, Göteborg, Sweden.

Liu, M., L. Siefferman, and G. E. Hill. 2007. An experimental test of female choice relative to male structural coloration in Eastern Bluebirds. Behavioral Ecology and Sociobiology 61:623–630.

Minolta Corporation. 1994. Precise color communication: color control from feeling to instrumentation, Minolta Corporation, Osaka, Japan.

Møller, A. P., 1994. Sexual selection and the Barn Swallow. Oxford University Press, Oxford, England.

Piper, W. H., and R. H. Wiley. 1990. The relationship between social dominance, subcutaneous fat, and annual survival in wintering White-throated Sparrows (*Zonotrichia albicollis*). Behavioral Ecology and Sociobiology 26: 201–208.

Prum, R. O. 2006. Anatomy, physics, and evolution of structural colors, p. 295–353. *In* G. E. Hill and K. J. McGraw [eds.], Bird coloration, volume 1: mechanisms and measurements. Harvard University Press, Cambridge, MA.

Pyle, P., S. N. G. Howell, R. P. Yunick , and D. DeSante. F. 1987. Identification guide to North American passerines. Slate Creek Press, Bolinas, CA.

Quesada, J., and J. C. Senar. 2006. Comparing plumage colour measurements obtained directly from live birds and from collected feathers: the case of the Great Tit. Journal of Avian Biology 37:609–616.

Rémy, A., A. Grégoire, P. Perret, and C. Doutrelant. 2010. Mediating male–male interactions: the role of the UV blue crest colouation in Blue Tits. Behavioral Ecology and Sociobiology 64:1839–1847.

Rohwer, S. A. 1975. The social significance of avian winter plumage variability. Evolution 29:593–610.

Rohwer, S. A. 1982. The evolution of reliable and unreliable badges of fighting ability. American Zoologist 22:531–546.

Senar, J. C. 2006. Color displays as intrasexual signals of aggression and dominance, p. 87–136. *In* G. E. Hill and K. J. McGraw [eds.], Bird coloration, volume 2: function and evolution. Harvard University Press, Cambridge, MA.

Senar, J. C., and M. Camerino. 1998. Status signalling and the ability to recognize dominants: an experiment with siskins (*Carduelis spinus*). Proceedings of the Royal Society of London B 265: 1515–1520.

Senar, J. C., J. Domènech, and M. Camerino. 2005. Female siskins choose mate by the size of the yellow wing stripe. Behavioral Ecology and Sociobiology 57:445–469.

Senar, J. C., J. J. Negro, J. Quesada, I. Ruiz, and J. Garrido. 2008. Two pieces of information in a single trait?: the yellow breast of the Great Tit reflects both pigment acquisition and body condition. Behaviour 145:1195–1210.

Senar, J. C., V. Polo, F. Uribe, and M. Camerino. 2000. Status signalling, metabolic rate and body mass in the siskin: the cost of being a subordinate. Animal Behaviour 59:103–110.

Sheldon, B. C., S. Andersson, S. C. Griffith, J. Örnborg, and J. Sendecka. 1999. Ultraviolet colour variation influences Blue Tit sex ratios. Nature 402: 874–877.

Siefferman, L., and G. E. Hill. 2005a. UV-blue structural coloration and competition for nestboxes in male Eastern Bluebirds. Animal Behaviour 69:67–72.

Siefferman, L., and G. E. Hill. 2005b. Evidence for sexual selection on structural plumage colouration in female Eastern Bluebirds (*Sialia sialis*). Evolution 59:1819–1828.

Siitari, H., J. Honkavaara, E. Huhta, and J. Viitala. 2002. Ultraviolet reflection and female mate choice in the Pied Flycatcher, *Ficedula hypoleuca*. Animal Behaviour 63:97–102.

Smith, S. M. 1994. Social influences on the dynamics of a northeastern Black-capped Chickadee population. Ecology 75:2043–2051.

Vedder, O., E. Schut, M. J. L. Magrath, and J. Komdeur. 2008. Ultraviolet crown colouration affects contest outcomes among male Blue Tits, but only in the absence of prior encounters. Functional Ecology 24:14–175

Vedder, O., P. Korsten, M. J. L. Magrath, and J. Komdeur. 2010. Ultraviolet plumage does not signal social status in free-living Blue Tits: an experimental test. Behavioral Ecology 19:410–416.