

# Here comes the sun: multimodal displays are associated with sunlight incidence

Paula Sicsú · Lilian T. Manica · Rafael Maia ·  
Regina H. Macedo

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**Abstract** Conspicuousness of courtship signals in animals likely evolved to maximize mate attraction while minimizing predator detection. It is assumed, though largely unknown, that environmental and luminosity conditions affect the detectability of ornaments and motor displays and could thus strongly influence behavior. We combined visual models and behavioral observations to test whether the multimodal display of the blue-black grassquit (*Volatinia jacarina*) is influenced by environmental conditions, predicting that males should display more often in moments with high sunlight incidence upon their bodies. By displaying in such a context-dependent fashion, males would be able to maximize conspicuousness of their iridescent blue-black plumage and avoid displaying continuously, since the latter would involve higher energetic investment. We recorded the rates of both complete displays (leap with singing) as well as incomplete ones (singing while perched) for males during repeated 30-min focal observations in varying environmental situations in the field. We found that when bathed directly in sunlight, males increased their rates of displays, tending to exhibit more complete rather than incomplete displays in this condition and suggesting a potential trade-off between display types. Our results suggest that animals may adjust the timing and precise location of signal activity to improve the efficiency or likelihood of detection of some signal elements.

**Keywords** Blue-black grassquit · Contextual plasticity · Courtship · Iridescent plumage · Motor display · Sexual selection · Visual signals

## Introduction

The expression of avian ornamental traits reflects the strength of different selective pressures such as mate attraction and predator avoidance. Such visual signals can include coloration and motor displays, both of which have roles in inter- and intraspecific communication (reviewed in Andersson 1994; Searcy and Nowicky 2005). Adequate signal transmission from a sender to a receiver can only occur, however, if the signal is distinguishable from background environmental noise (Endler 1990, 1992, 1993; Uy and Endler 2004). An important means for increasing efficiency of transmitted information is to boost the signal's visibility. For instance, the conspicuousness of a trait such as a colored plumage patch naturally depends on environmental luminosity, which affects the amount of photons arriving on the retina of the animal observing the signal. The signal itself can be enhanced by the chromatic or achromatic (brightness) contrast of the visual signal with its background. Thus, ambient light may directly affect an animal's prominence relative to its surroundings. In addition to the color spectrum of a trait and its background, other important elements that may add to signal conspicuousness include pattern geometry and movement (Hailman 1977; Endler 1992, 1993; Fleishman 1992; Fleishman and Persons 2001; Ord et al. 2010; Wilgers and Hebets 2011). Thus, it is plausible that the chosen physical environment where an animal exhibits its signals will have a strong influence on the signal's detectability and, consequently, on successful communication.

Despite the apparent desirability of enhancing signal conspicuousness in some social contexts, the use of eye-catching signaling traits and motor displays comes at a cost, since these also increase visual detection by potential predators

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P. Sicsú · L. T. Manica · R. H. Macedo (✉)  
Departamento de Zoologia—IB, Universidade de Brasília,  
Brasília 70910-900, Brazil  
e-mail: rhfmacedo@unb.br

R. Maia  
Department of Biology, Integrated Bioscience Program,  
University of Akron, Akron, OH 44325-3908, USA

that hunt diurnally (e.g., Godin and McDonough 2003; Sullivan and Kwiatkowski 2007) or competitors that can gain some advantage by accessing the signal content (McGregor 1993). Thus, secondary sexual traits of males, including both visual ornaments as well as motor displays, should reflect a trade-off between gains through increased visibility to the intended viewer (e.g., females and rival males) and costs due to natural selection pressures (Fowler-Finn and Hebets 2011). Early empirical evidence for such a trade-off included studies of vertebrates and invertebrates in different habitats and substrates. Guppies *Poecilia reticulata* appear to increase courtship behavior in the early morning and late afternoon (Endler 1987), which are periods that coincide with light levels that could minimize predator detection while allowing intraspecific visual detection of color patterns (Endler 1991). Male ghost swift moths *Hepialus humuli* seem to have adaptive behaviors relative to ambient conditions and predation, restricting their sexual display flights to a relatively short window of time at dusk, when predation may be minimized despite the conspicuousness of their wing coloration (Andersson et al. 1998). Another example is the fiddler crab *Uca tangeri*, which exhibits conspicuous coloration in those body parts that are relevant for intraspecific communication but has fairly cryptic coloration in other parts that can be viewed by potential avian predators (Cummings et al. 2007). Motor displays can also be costly due to increased detection by predators: a laboratory manipulation showed that male wolf spiders *Pardosa milvina* that courted via leg raises were more likely to be preyed upon than those that did not court (Hoefer et al. 2008). Furthermore, animals invest time and occasionally considerable energy executing motor and acoustic displays at the expense of other vital functions (Wells and Taigen 1984; Sullivan and Kwiatkowski 2007).

Numerous studies have analyzed the spectral properties of male ornaments relative to the animal's substrate or to the visual sensitivity of potential predators or females (Endler and Théry 1996; Grill and Rush 2000; Macedonia 2001; Fuller 2002; Heindl and Winkler 2003; Leal and Fleishman 2004; Schultz et al. 2008). There has been less focus, however, on the idea that animals should optimize signaling transmission to become more noticeable by choosing the proper moments to display, although the theoretical framework encompassing optimization of signal transmission was proposed over 30 years ago (Hailman 1979). For example, empirical evidence shows that many bird species have the behavioral plasticity to optimize the timing and placement, as well as the properties, of their vocalizations in noisy environments (reviewed in Brumm and Slabbekoorn 2005). Additionally, recent work has targeted the changes in timing, volume, or pitch of bird song to overcome noise pollution (Gross et al. 2010; Cardoso and Atwell 2011; Francis et al. 2011). However, very little is known about plasticity in signal transmission beyond the acoustic modality. Some

authors have suggested that animals should orient their bodies or color patches to optimize visualization within specific contexts of their environment (Endler and Théry 1996; Doucet and Montgomerie 2003), an idea that received recent empirical support in a study with great bustards *Otis tarda* (Olea et al. 2010) and in one with snowy owls *Bubo scandiacus* (Bortolotti et al. 2011). Another study with two *Anolis* species has also shown that individuals increase the speed of their territorial displays as a function of background motion due to windblown vegetation (Ord et al. 2007).

One spectacular type of coloration that is strongly influenced by lighting conditions is iridescent coloration, which is found in a wide range of taxa, from beetles and several other invertebrates (notably butterflies) to vertebrates such as fishes and birds, among others (reviewed in Doucet and Meadows 2009). Iridescent plumage color results from the coherent scattering of light waves by nanostructural elements of feather barbules, namely keratin, melanin and air, organized in layered or crystalline arrangements (Prum 2006; Doucet and Meadows 2009). Iridescent colors change in appearance based both upon viewing geometry as well as illumination (Osorio and Ham 2002). For example, iridescent coloration reflects maximally at a specular geometry, and thus appears much brighter when directly illuminated rather than under diffuse light, and the total amount of light can change the intensity of iridescent colors (Osorio and Ham 2002). Therefore, the appearance of iridescent colors can be largely controlled by individual choice of where and when to display it, making it an ideal trait to evolve associated to context-dependent behavioral execution of courtship displays.

Here, we examined behavioral plasticity in the execution of the multimodal sexual display of the blue-black grassquit *Volatinia jacarina* (Fig. 1) in face of fluctuating environmental conditions. The blue-black grassquit is a passerine that inhabits grasslands, disturbed areas, and savannas in the Neotropics and is very abundant in Brazil. Females and juveniles are brownish and cryptic, as are adult males during the non-breeding season. At the beginning of the breeding season, adult males molt into a nuptial blue-black plumage that is UV-shifted in coloration (peaks in UV and violet blue wavelengths) and also strikingly iridescent (Maia et al. 2009; Maia and Macedo 2010). They perform a multimodal display to attract females and defend their small territories (ca. 13–72 m<sup>2</sup>; Almeida and Macedo 2001). The courtship display can occur either as (1) a motor exhibition that involves leaps accompanied by a vocalization (hereafter called “complete display”); or (2) alternatively, the display can include only the vocalization while perched, without the motor component of the leap (hereafter called “incomplete display”). The complete displays are executed usually from an elevated perch and leaps can reach a height of approximately 25 cm (Costa and Macedo 2005), during which males flap their

wings several times, snapping them behind their backs while exposing white underwing patches (Fig. 1). The motor part of the display is produced almost simultaneously with a short, buzzing vocalization that initiates during the leap and ends when the bird is landing back on its perch. Males generally produce the complete display at rates that range from 1.8 to as many as 12.3 per minute (Almeida and Macedo 2001), and these are executed hundreds of times each day throughout the long breeding season of approximately 6 months (Carvalho et al. 2007). Although males invariably produce the vocalization when they leap, they frequently produce only the incomplete display, in which they vocalize without leaping. Males use deciduous vegetation for their display perches, usually shrubs and small trees scattered over the open grassland, and are thus exposed to strong variation in ambient light and other meteorological



**Fig. 1** A male blue-black grassquit (*Volatinia jacarina*) executing its leaping display in central Brazil. Photo by Rafael Maia

variables such as wind and rain. As yet, it is unknown whether social and environmental conditions influence the execution of complete or incomplete displays. Blue-black grassquit complete displays are extremely vigorous and likely to be very energetically costly.

Here, we combine empirical observations under natural conditions with visual models to test whether blue-black grassquits modulate their behavior in order to maximize their investment according to the conspicuousness of their visual displays. Assuming that leaping displays are energetically costly, that iridescence plays an important role in making the display highly visible, and that direct sunlight substantially increases the conspicuousness of iridescent plumage, we predicted that males would produce displays at higher rates in moments of direct incidence of sunlight upon their bodies. We anticipated that the execution of complete displays would occur in moments of higher sunlight incidence and incomplete displays (only vocalizations while perched) in moments with lower sunlight incidence. We also analyze rates of displays relative to other environmental variables, since other factors (e.g., temperature, relative humidity, and sun height) could also be assumed to affect the execution of displays. For instance, birds are known to become less active when temperatures increase, and this occurs usually when sunlight is more intense (i.e., increasing sun height from horizon). Additionally, relative humidity also plays a role in determining display rate, since respiratory dehydration may occur if the bird is heat-stressed due to elevated temperatures and the air is extremely dry (see Altshuler and Dudley 2006).

## Materials and methods

### Behavioral observations

The study was conducted from November 2009 to February 2010 at the Fazenda Água Limpa, a property belonging to the University of Brasilia, in central Brazil (15°56' S, 47°56' W). We mist-netted and color-banded male blue-black grassquits early in the breeding season, and these were released immediately in the same place where they were captured. Of captured males, 21 established territories within the study area. We conducted repeated focal observations of these males between 0600 and 1130 h for a maximum of 35 min for each observation, during which two observers recorded all events of complete (with leap) and incomplete (perched singing) displays at a distance of roughly 10–20 m from each bird. We obtained two focal observation periods for six males and three focal observation periods for 15 males, totaling approximately 1,500 h of observation of displaying males. Focal observation periods were subdivided into samples of 5-min intervals. The number of samples within focal observations ranged from two to seven (i.e.,

from 10 to 35 min), but most focal observations had six samples ( $n=37$ ), with the following distribution: two samples ( $n=6$  focal observations), three samples ( $n=4$ ), four samples ( $n=2$ ), five samples ( $n=4$ ), six samples ( $n=37$ ), and seven samples ( $n=4$ ). This resulted in a total of 298 samples within focal observation periods. Considering all focal observations, males were sampled from six to 19 times (mean $\pm$ SD = 14.19 $\pm$ 4.12 samples per male).

#### Environmental variables

Environmental variables were assessed by collecting data at the beginning and end of the 5-min sample intervals, and mean values were calculated for each variable for each interval. We measured four variables (see details below): ambient temperature, relative air humidity, direct incidence of sunlight upon the bird, and sun height at the moment of observation relative to horizon level. Direct observation of the bird allowed us to determine whether there was direct incidence of sunlight upon the bird's body at the beginning and end of each 5-min interval. We classified sunlight incidence in three categories: high incidence when the bird was in direct sunlight at the beginning and end of the interval; intermediate incidence when the bird was in direct sunlight either at the beginning or at the end of the interval, but not both; and low incidence when there was no direct sunlight upon the bird at both moments. Although this is a method that is somewhat imprecise, given that a bird could stop displaying in the first and last second of a 5-min interval resulting in a biased classification, we consider that the incidence of such errors should have been very small. Furthermore, the distribution of such errors would be completely random, cancelling out any directional bias. Finally, sun height was estimated by using the angular coordinate of the sun's vertical elevation from the horizon at the observation site, and was obtained from the National Oceanic and Atmospheric Administration (USA) site (NOAA, <http://www.esrl.noaa.gov/gmd/grad/solcalc/>). Information used to obtain the latter data included field site location, date, and exact time of each focal sample observation.

#### Statistical analyses

To analyze our data, we used measurements collected during each 5-min sample interval as a replicate. We included ambient temperature, relative humidity, and sun height in a principal component analysis (PCA) to reduce potential effects of correlations among these variables ( $r_{\text{temp} \times \text{humid}}=-0.82$ ,  $r_{\text{temp} \times \text{sun height}}=0.80$ , and  $r_{\text{humid} \times \text{sun height}}=-0.70$ ), using "princomp" function in R software (R Development Core Team 2011). Relative humidity was log-transformed to approximate a normal distribution. For subsequent analyses, we used the first principal component

(PC1, proportion of variance=85.2 %) as a single measure of these three meteorological variables. Higher values of PC1 represent higher values of all variables, except relative humidity (loadings—0.59, -0.57, and 0.57; and correlations with PC1—0.95, -0.91, and 0.90 for temperature, relative humidity, and sun height, respectively).

We tested the influence of meteorological measurements (represented by PC1) and sunlight incidence on males (low, high, and intermediate) upon male complete or incomplete display rates (number of leaps with vocalizations and number of vocalizations while perched per 5 min, respectively) using a linear mixed model (LMM). LMM was fitted by restricted maximum likelihood using the "lme4" R package (Bates et al. 2011), including display rate as response variable and display type (complete or incomplete), light incidence, PC1, and the interactions of display type with light incidence and PC1 as predictors. To eliminate the possible interference of non-independence of the data, since sampling of each male occurred in different focal observations, we included a nested hierarchical random effect: focal observation nested within male identity. Statistical significances of predictor terms were generated by comparing a full model with a restricted model, in which the predictor of interest was excluded, using a likelihood ratio test. Likelihood ratio statistics in Table 1 represent the deviance between log-likelihood of models, and the degrees of freedom represent the change in number of extra parameters in the full model. Tukey's comparisons between levels of variables, when statistically significant, were developed using the "glht" function in the "multcomp" R package (Hothorn et al. 2008). Significant levels were set at 5 % and Bonferroni corrections were applied in post hoc multiple comparison analyses.

We evaluated the presence of outliers in the response and explanatory variables by plotting values against observations grouped by male identity. We tested normality of response variables and homogeneity of variances using Shapiro–Wilk tests and residual analyses (standardized residuals versus fitted values scatter plots), respectively. Sample sizes differ among meteorological variables because missing data occurred for several observations. Results are presented as mean $\pm$ SD, unless otherwise noted.

#### Visual modeling

Based on the results from the behavioral experiments, we evaluated the conspicuousness of the blue-black iridescent plumage of grassquits against a natural background using a tetrachromatic visual model (Vorobyev and Osorio 1998; Vorobyev et al. 1998). We used an avian visual model where color discrimination is a function of the received signal, and limited by photoreceptor and neural noise (Vorobyev and Osorio 1998; Osorio et al. 2004) to describe chromatic and brightness discrimination as a function of feather reflectance,

**Table 1** Results from LMM of display rates of blue-black grassquit males with the display type (complete or incomplete), light incidence levels and environmental variables represented by a principalcomponent PC1 as fixed factors, controlled for repeated samples within males and focal observations ( $n=298$  samples)

Predictor	Standardized coefficient (SE)	$\chi^2$	<i>df</i>	<i>p</i> value
Intercept	0.01 (0.11)			
Light incidence <sup>a</sup>		14.10	4	0.007
Intermediate	0.19 (0.16)			
High	0.45 (0.14)			
PC1	-0.05 (0.04)	1.57	2	0.46
Display type <sup>b</sup>		39.47	4	<0.001
Incomplete	-0.39 (0.10)			
Display type $\times$ light incidence		4.83	2	0.09
Incomplete $\times$ intermediate	0.23 (0.20)			
Incomplete $\times$ high	-0.24 (0.16)			
Display type $\times$ PC1	0.03 (0.04)	0.55	1	0.46

Variances  $\pm$  SE of random effects: male identity=0.07 $\pm$ 0.02, focal observation nested within male identity=0.07 $\pm$ 0.01

<sup>a</sup> Low, intermediate, or high. Estimates are relative to the low level

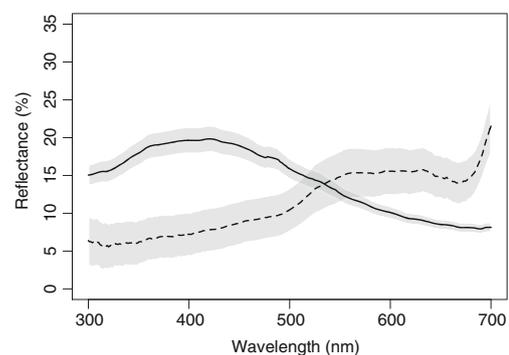
<sup>b</sup> Complete (leaps with vocalization) or incomplete (vocalizations while perched). Estimates are relative to the complete displays level

ambient illumination, and background color. Nuptial plumage reflectance was obtained from five dorsal feathers collected from 43 captured males, 19 of which were monitored in focal observations during the present study (Fig. 2). We measured reflectance with an Ocean Optics USB4000 spectrometer attached to a PX-2 pulsed xenon light source (range 250–750 nm; Ocean Optics, Dunedin, FL, USA). Feathers were taped to a black velvet surface to simulate natural arrangement on the bird's body. Reflectance was measured with the probe held at 45° and attached to a holder to exclude ambient light, at 6 mm from the feather surface. We measured reflectance relative to a WS-1-SS white standard and using the black surface as a dark reference. For each feather, we recorded 50 sequential spectra, and repeated three times between samples by changing the position of the probe between readings to guarantee we were measuring different parts of the feather. We calculated plumage reflectance as an average of the three measurements at 1-nm steps between 300 and 700 nm. To assess the natural luminosity background for the blue-black grassquits, we took reflectance measurements from 20 leaves and 20 branches from the vegetation where grassquits were observed executing their displays, which were averaged to characterize the background color (Fig. 2).

Following Vorobyev et al. (1998), we calculated cone quantum catch for each of the four avian cones as the summed product of plumage reflectance, the ambient illuminant, and the absorbance spectrum of the cone across the wavelengths of the avian visual spectrum (300 to 700 nm; equation 1 in Vorobyev et al. 1998). We log-transformed quantum catches to make the differences in cone stimulation proportional to their magnitudes (Weber–Fechner law,

equation 4 in Vorobyev et al. 1998). Since the cone sensitivity functions for the blue-black grassquit are unknown, we used the average UV-sensitive curves described in Endler and Mielke (2005), but we also compared the results to those obtained considering the average V-sensitive curves described in the same study. Since the results were qualitatively identical, we report only the results for the UV-sensitive curves. For the luminance values, we used the “blue sky” illuminant from Endler (1993). Though the overall intensity of luminance may vary among different sites, the spectral shape of illuminant curves under the same ambient light conditions are roughly similar (Endler 1993), and fine-scale differences are unlikely to affect contrast calculations due to color-correction mechanisms of the visual system (Stoddard and Prum 2008).

We then calculated the contrast between the plumage and the background as a function of the adjusted log-transformed



**Fig. 2** Reflectance spectra of male blue-black grassquit feathers (*solid line*) and the natural background (*dashed line*). The *gray shaded band* represents the 95 % confidence interval

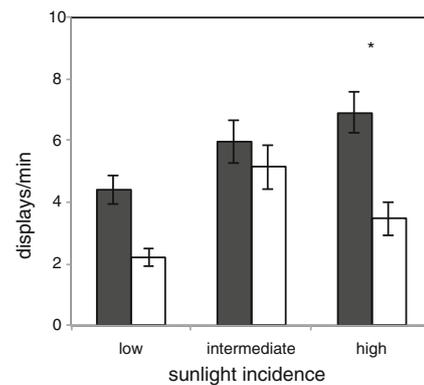
quantum catches weighted by the noise in each receptor channel (Vorobyev and Osorio 1998; Osorio et al. 2004). For the chromatic contrast ( $\Delta S$ ), we assumed a noise-to-signal ratio of a single cone that yielded a Weber fraction of 0.05 for the long-wavelength sensitive cone, and the relative density of the UV, short-, medium-, and long-wavelength sensitive cones to be 1:2:2:4 (as estimated from the Pekin robin *Leiothrix lutea*; Maier and Bowmaker 1993). Achromatic contrast ( $\Delta L$ ) was calculated following Siddiqi et al. (2004) and also assuming a Weber fraction of 0.05. To account for differences in light intensity, we considered scenarios of dim and bright illumination by scaling the quantum catches assuming a flux of 500 photons per integration time for the dim-light condition (where contrast thresholds are dominated by photon noise) and  $10^4$  photons per integration time for the bright condition (Vorobyev 2003; Osorio et al. 2004).

All color analyses were conducted in R using the “pavo” package (Maia et al. 2013). Differences in chromatic and achromatic contrasts were assessed using linear mixed models of  $\Delta S$  and log-transformed  $\Delta L$  with light intensity as a fixed factor and male identity as a random effect.

## Results

For the 21 males observed, complete display rates (leaps with song/min) varied from 0 to 19.8 leaps/min ( $5.47 \pm 6.08$ ) and incomplete display rates (songs without leap/min) from 0 to 23.8 songs/min ( $3.2 \pm 4.52$ ). General environmental patterns during focal observations varied widely and can be described by the following parameters: temperatures ranged from 14 to 36.9 °C ( $23.9 \pm 4.7$ ), relative humidity from 35.9 to 93.7 % ( $71.18 \pm 13.3$ ), and sun height from  $-1.84$  to  $65.6^\circ$  ( $25.40 \pm 16.53$ ). Considering all samples, 51.01 % ( $n=152$ ) were obtained under low levels of sunlight incidence, 31.54 % ( $n=94$ ) under intermediate levels and, 17.45 % ( $n=52$ ) under high levels.

The incidence of direct sunlight upon males affected their display rates, and at high sunlight incidence levels males performed more displays compared with males in low levels of sunlight incidence ( $z=3.16$ ,  $p=0.005$ ; Table 1). Display rates in intermediate levels of sunlight incidence did not differ from those in low and high levels of sunlight incidence ( $z=1.21$ ,  $p=0.67$  and  $z=1.58$ ,  $p=0.34$ , respectively; Table 1, Fig. 3). At each level of sunlight incidence, males executed higher rates of complete displays than incomplete displays (Table 1) and this difference tended to be larger at high levels of sunlight incidence, but the interaction between display type and sunlight incidence level did not reach statistical significance (Fig. 3). Meteorological variables represented by PC1 had no effect on display rates or on the type of display exhibited (Table 1).



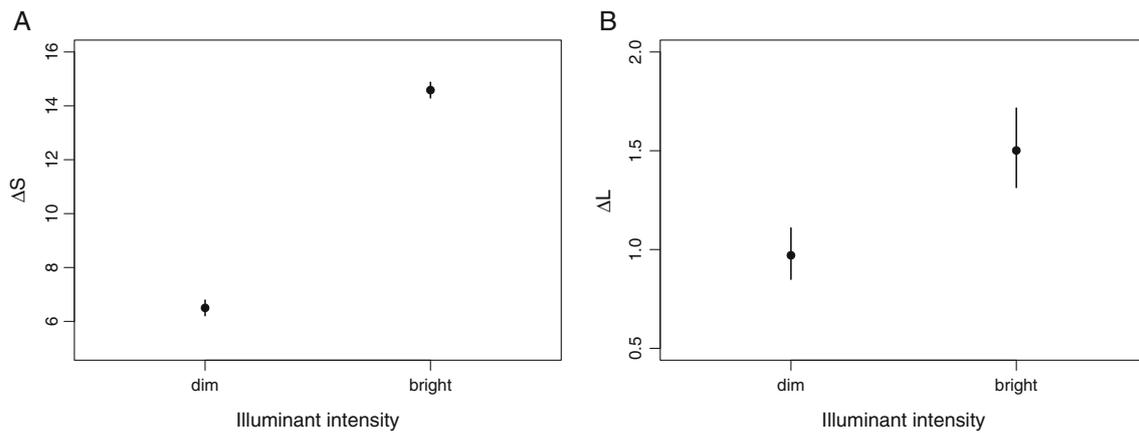
**Fig. 3** Rates of complete displays (leaps synchronized with songs, *dark columns*) and incomplete displays (songs without leaps, *white columns*) of blue-black grassquit males in different levels of sunlight incidence. Bars represent standard errors and the *asterisk* (\*) represents statistical significance for post-hoc paired comparison of light incidence levels at  $p < 0.001$

Both the chromatic contrast ( $\Delta S$ , Fig. 4a) and the achromatic contrast ( $\Delta L$ , Fig. 4b) between the blue-black grassquit plumage and its habitat background differed between the light intensity conditions, showing a higher contrast under brighter lighting (Table 2). These results indicate that the blue-black coloration and the brightness of the nuptial plumage of blue-black grassquit males become more evident relative to the background when light intensity is higher (Fig. 4).

## Discussion

Our study reveals that the courtship motor and acoustic displays of male blue-black grassquits are modulated by their exposure to direct sunlight. We found that when sunlight incidence upon a male was high, the display behavior was exhibited at a much higher rate when compared with rates at lower levels of sunlight incidence. Furthermore, males tended to show increased rates of the motor part of the display at higher sunlight levels and reduced their rates of acoustic displays under this condition. Among all the environmental variables measured, only direct incidence of sunlight modified the patterns of the multimodal display of the blue-black grassquit. Thus, results suggest that plumage iridescence is likely to be highly visible when the bird is directionally illuminated. These results are supported by the visual models, which show that light intensity over male iridescent plumage significantly increases its conspicuousness, both in chromatic (hue and saturation) and achromatic (brightness) aspects of the coloration. Given that the motor display is likely to be very costly, it should compensate the bird to leap preferentially when bathed in sunlight and there is a greater chance of being seen by conspecifics.

We suggest that there is a trade-off between display types depending upon the presence of direct sunlight. In low and



**Fig. 4** Chromatic (a) and log-transformed achromatic (b) contrast of the male blue-black grassquit iridescent plumage coloration against a natural background, as a function of the intensity of ambient illumination, inferred from visual models of avian vision. Bars represent 95 % confidence intervals

intermediate sunlight incidence, both the complete and incomplete display rates are lower than in conditions of higher sunlight incidence. When high light incidence occurs, the birds tend to decrease the rate of incomplete display in favor of executing the complete motor displays. These observed patterns suggest that the birds shift from a low-gear display mode (alternation of only vocalizing and vocalizing with leaps) to a high rate of leaping. Evidently, this overall pattern should be quite variable at the individual level, given that males differ in overall condition and specific circumstance (e.g., breeding status, nearby rivals, or females).

These are striking results for two reasons. First, because this evidence suggests that the iridescent coloration of the blue-black grassquit's plumage is a crucial element used in intraspecific communication. Iridescent colors in the blue-black grassquit are produced by a thin-film of keratin over an array of organized melanin granules (melanosomes; Maia et al. 2009). These types of colors are dominated by a strong specular component (i.e., reflected at the same but opposite angle of incident light) and have negligible diffuse (scattered across all angles) reflectance (e.g., Maia et al. 2011), such

that if there is no direct light from a point source, color properties are virtually unnoticeable (Osorio and Ham 2002; Doucet and Meadows 2009). Since direct rather than diffuse light results in iridescent plumage seeming brighter (Osorio and Ham 2002), the leaping behavior may function primarily to optimize transmission of the information conveyed by this specific plumage characteristic (but see below for alternative possibility).

Further, even if these directional aspects of reflectance geometry are ignored, the spectral properties of direct incident light cause the blue-black color of male nuptial plumage to be more noticeable and conspicuous against the background, as shown by the results from the visual models. It is interesting to note that both the chromatic and achromatic attributes were affected by lighting conditions. Given that the chromatic attributes are influenced by investment in the speed of molting in this species (Maia and Macedo 2010), this context-dependent investment in complete displays may therefore increase the signal value of these condition-dependent attributes of plumage color. Although the developmental self-assembly of iridescent feather nanostructures

**Table 2** Results from LMM of chromatic ( $\Delta S$ ) and achromatic ( $\Delta L$ ) contrasts between the plumage reflectance and the background in different light intensities, controlled for repeated measurement of males ( $n=129$  samples from 43 males)

Response variable	Predictor	Estimate (SE)	<i>F</i>	<i>df</i>	<i>p</i> value
$\Delta S^1$	Intercept	14.58 (0.15)			
	Intensity <sup>a</sup>		12,065.24	1, 42	<0.001
	Dim	-8.08 (0.07)			
$\Delta L^{2,3}$	Intercept	0.41 (0.07)			
	Intensity <sup>a</sup>		25,988.19	1, 42	<0.001
	Dim	-0.44 (0.01)			

Variance  $\pm$  SE of random effect (male identity): <sup>1</sup> 0.91 $\pm$ 0.14, <sup>2</sup> 0.45 $\pm$ 0.07, <sup>3</sup> log-transformed

<sup>a</sup> Dim and bright. Estimates are relative to bright level

is unlikely to be energetically demanding, developmental conditions necessary for it to occur could conceivably be disrupted by physical or social stressors (McGraw et al. 2002; Maia et al. 2012a, b). Other elements of the multimodal display, including motor and song attributes, may be important in transmitting specific information about the male, but are less likely to be affected by the direct incidence of sunlight. Thus, the nature of plumage attributes as an indicator of male developmental quality is likely an important aspect of this motor display, with the most favorable exhibition of iridescence, however, depending upon the leaping part of the display. Future studies should experimentally investigate the relative importance of the motor and color components of this complex display (e.g., Macedonia et al. 2013).

Alternatively, we could also interpret our results to indicate that the information content of the signal is contained in the leap itself (e.g., male vigor and/or skill) and that the iridescence serves the function of enhancing the leap, making it more visible (see Byers et al. 2010). Thus, the multimodal display of the blue-black grassquit involves interdependent components that may convey different information contents, and efficient transmission of the signal may be enhanced by behavioral modulation according to environmental conditions. Independent of whether we apply one or the other of the above explanations (the leap exposes the iridescence or the latter enhances the leap), our results in this study support the general prediction that animals adjust behaviorally to their environment to increase signal conspicuousness used for communication with nearby conspecifics.

A second noteworthy point involves the dynamic transition from the passive display mode to the energetically costly leaping display, which suggests a remarkable behavioral flexibility that is in line with expectations concerning signal evolution. The adjustment of different signal components involving trade-offs has been found primarily for males of different taxa in response to the presence and reproductive condition of females (Gibson and Bradbury 1985; Kelso and Verrell 2002; Patricelli et al. 2002; Patricelli and Krakauer 2009). Here, we found that male blue-black grassquits modulate their courtship signal dynamically with subtle shifts in environmental cues. To our knowledge, only one study has examined the association between courtship displays and direct incidence of sunlight, suggesting that male peafowl *Pavo cristatus* maximize the efficacy of their displays by orienting themselves at about 45° to the right of the sun azimuth (Dakin and Montgomerie 2009). A postural change such as exhibited by peafowl probably involves negligible energetic costs to the animal. However, the energetic costs of modifying display mode to include vigorous movements (such as leaping) relative to presence of direct sunlight are likely to be very high for any species, even for small birds such as grassquits. In addition, while perched, blue-black

grassquits exhibit a uniform color pattern over their entire bodies, while when leaping they exhibit a dramatic contrast between underwing white patches and their black plumage. Therefore, for this species, subtle postural differences in body orientation may not have as strong an effect for signal transmission as obtained through the leaping display; however, confirmation of this possibility remains to be determined.

Early evidence suggested that there should be great variation and flexibility in signal optimization to match conditions encountered by animals (Endler 1991; Endler and Théry 1996). Although many studies have examined transmission optimization of acoustic signaling, many fewer studies have focused on how animals time and place motor or multimodal signals relative to their habitats, ambient light, or predation risk. These studies provided evidence that in many species visual signals and fixed daily activity patterns may have evolved to match a given physical landscape and specific ambient light conditions. We propose that, additionally, sexual selection has generated courtship behaviors in many species that allow instantaneous optimization of sexual signaling. Such behavioral contextual plasticity should be strongly selected for in species where the displaying behavior is costly, either energetically or because of increased risk of predation, and when an environmental cue can significantly modify signal quality and detectability.

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