Viewing geometry affects sexual dichromatism and conspicuousness of noniridescent plumage of Swallow Tanagers (Tersina viridis)

Authors: Barreira, Ana S., García, Natalia C., Lougheed, Stephen C., and Tubaro, Pablo L.

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RESEARCH ARTICLE

Viewing geometry affects sexual dichromatism and conspicuousness of noniridescent plumage of Swallow Tanagers (*Tersina viridis*)

Ana S. Barreira,[1]* Natalia C. García,[1] Stephen C. Lougheed,[2] and Pablo L. Tubaro[1]

[1] División Ornitología, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" - CONICET, Ciudad Autónoma de Buenos Aires, Argentina
[2] Department of Biology, Queen's University, Kingston, Ontario, Canada
* Corresponding author: abarreira@macn.gov.ar

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ABSTRACT

Some types of plumage color are difficult to characterize spectrophotometrically because the properties of the reflected light change with viewing geometry (i.e. the relative positions of the light source and the observer, and the orientation of the feather). This is the case for the noniridescent plumage coloration of the Swallow Tanager (*Tersina viridis*), which seems to change from a human perspective as the angle between the light source and the observer varies. In this study, we measured plumage reflectance with different angles of illumination and/or observation, and used avian visual models to evaluate the change in sexual dichromatism and conspicuousness with viewing geometry from a bird's perspective. We also calculated different color parameters to assess how these changed with viewing conditions. Sexual dichromatism showed large changes, with its maximum coinciding with the angle combination between illuminant and observer that produced both the highest conspicuousness for males and the highest crypsis for females. The conspicuousness of males also varied with viewing geometry, and was consistently less when viewed by the visual system of a potential avian predator (VS) than by that of a conspecific (UVS). The change in perceived coloration was mainly related to large variation in hue and chroma in the plumage of males as the relative angle between the illumination and observation probes changed. Our results show that viewing geometry can alter color perception, even for noniridescent plumage coloration. Therefore, the relative position of the light source and the observer should be considered in studies of avian visual communication, particularly for species with plumage coloration similar to that of Swallow Tanagers.

Keywords: plumage coloration, sexual dichromatism, conspicuousness, viewing geometry, Swallow Tanager, *Tersina viridis*, double scattering

La geometría de visualización afecta el dicromatismo sexual y la conspicuidad de la coloración del plumaje no iridiscente de *Tersina viridis*

RESUMEN

Algunos tipos de colores del plumaje son difíciles de caracterizar espectrofotometricamente debido a que las propiedades de la luz que reflejada varían con la geometría de visualización (es decir, la posición relativa de la fuente lumínica, el observador y la pluma). Este es el caso de la coloración no-iridiscente de la *Tersina viridis*, que parece cambiar desde la perspectiva humana al modificarse el ángulo conformado entre el observador y la fuente de luz. En este trabajo medimos la reflectancia del plumaje con diferentes ángulos de iluminación y/o observación y empleamos modelos visuales avianos para evaluar el cambio en dicromatismo sexual y conspicuidad. También calculamos parámetros descriptores de la coloración para determinar cómo cambian éstos en función de la geometría de visualización. El dicromatismo sexual mostró una amplia variación, siendo máximo con la combinación de ángulos entre iluminante y observador que también produjo el máximo de conspicuidad en los machos y el máximo de cripsis en las hembras. La conspicuidad de los machos también varió con la geometría de visualización y además fue consistentemente menor para sistemas visuales avianos menos sensibles al UV (como los de los máximos potenciales predadores de esta especie) que para sus conspecíficos, que serían más sensibles a longitudes de onda del UV. El cambio percibido en la coloración estuvo principalmente relacionado a una gran variación en el tono y la saturación en el plumaje de los machos al cambiar el ángulo conformado entre la fuente lumínica y el observador. Nuestros resultados muestran que la geometría de visualización puede alterar la percepción del color, aún en plumajes no-iridiscentes. Por lo tanto, es importante considerar la posición relativa de la fuente de luz y el observador en estudios de comunicación visual en aves, particularmente en especies con coloración del plumaje como la de la *Tersina viridis*.

Palabras clave: coloración del plumaje, dicromatismo sexual, conspicuidad, geometría visual, *Tersina viridis*, dispersión doble

INTRODUCTION

Plumage coloration patterns in birds are the subject of intense study because of their roles in sexual selection and detection by potential predators (Dunn et al. 2015). Avian visual capabilities differ from those of humans as birds are able to see ultraviolet (UV) colors, to which humans are blind, and have a higher color discriminatory capacity. This is the result of the presence of a fourth cone in their retinas that is sensitive to UV light and a system of oil droplets associated with their photoreceptors (Bowmaker et al. 1997, Cuthill et al. 2000). To address the limitations of human vision–based measurements, light reflectance has been extensively used to objectively describe plumage coloration and its variation (Bennett et al. 1994, Montgomerie 2006). Moreover, avian visual models (Vorobyev and Osorio 1998, Endler and Mielke 2005, Stoddard and Prum 2008) have been increasingly applied to describe color reflectance as perceived by birds (Eaton 2005, Stoddard and Prum 2008, Burns and Shultz 2012).

Some plumage colors are difficult to quantify, even with these broadly employed spectrophotometric methods, because they vary with viewing geometry (i.e. the position of the observer relative to the light source; Osorio and Ham 2002, Meadows et al. 2011). This is true for iridescent coloration, such as that observed in hummingbirds, the tail of male Indian Peafowl (*Pavo cristatus*), and the neck of some pigeons, for example, which varies in perceived hue as the illuminating and/or observation angles change in relation to the orientation of the feather (Prum 2006). To quantify variation in iridescent plumage that is biologically meaningful thus requires different measurement techniques (Osorio and Ham 2002, Meadows et al. 2011, Van Wijk et al. 2016). Most noniridescent structural feather colors show little or no variation in hue with viewing geometry under omnidirectional illumination conditions (Prum 2006); this is because light is reflected from the isotropic internal keratin structure of the feather in all directions equally (Saranathan et al. 2012). However, a few structurally produced and noniridescent feather colors do show considerable hue variation when the observation angle changes relative to the light source; this phenomenon is termed diffuse coloration (Osorio and Ham 2002) and is poorly understood.

The plumage of the Swallow Tanager (*Tersina viridis*) affords an excellent study system for understanding structurally produced noniridescent coloration that shows considerable change with viewing geometry, even under natural illumination, at least from the human visual perspective. This species exhibits high sexual dichromatism, with males having blue plumage and females green, although males have an unusual pattern of reflectance with a double peak (one main peak in green wavelengths and a secondary peak located in the UV range; Barreira et al. 2008). Schaefer (1953:404) described the male Swallow Tanager as "*... nearly entire body turquoise blue, if seen against the light in bright sunshine, but changing to emerald green when seen with the light*" (Appendix Figure 5). The observed color change of male Swallow Tanagers is not equivalent to iridescence because it does not depend on the orientation of the feather in relation to the observer or the light source (Prum 2006), but rather the angle between the two. This phenomenon is purportedly the result of double scattering within the internal keratin nanostructure of feather barbs (Noh et al. 2010, Saranathan et al. 2012). Double scattering has been described by Saranathan et al. (2012) in a wide range of species with structurally based plumage coloration, including nonpasserines (Coraciiformes and Psittaciformes), many passerine families (Pittidae, Contingidae, Pipridae, Paradisaeidae, Irenidae, and Fringillidae), and many genera within Thraupidae (*Tersina*, *Dacnis*, *Tangara*, and *Thraupis*; Appendix Figure 6).

The males of some species with iridescent plumage can increase the visibility of their displays by selecting specific viewing geometry and lighting conditions when conducting their sexual displays (Dakin and Montgomerie 2009, Sicsú et al. 2013), which can greatly affect their mating success (Dakin and Montgomerie 2013). Evidence suggests that individual birds can increase or decrease their exposure to others by displaying under specific viewing conditions (Uy and Endler 2004, Dakin and Montgomerie 2009, 2013, Sicsú et al. 2013). Despite the diverse set of species in which double scattering has been registered by analysis of their plumage reflectance properties and production mechanisms (Osorio and Ham 2002, Noh et al. 2010, Saranathan et al. 2012), the effect of viewing geometry on their visibility to predators or conspecifics, to the best of our knowledge, has never been assessed. Here, we hypothesize that viewing geometry will affect both the sexual dichromatism and the conspicuousness of the Swallow Tanager, and we speculate as to the biological significance of this in the wild. We employ standardized, objective, and quantitative techniques of measurement to assess how these 2 factors vary from an avian perspective.

METHODS

We conducted this study using museum skins of the Swallow Tanager deposited at the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia." We only employed specimens in an excellent state of preservation as determined by close visual examination, with no signs of color fading or preparation defects (i.e. plumage was not stained, feathers were not evidently missing, and color did not looked degraded), and with complete information on sex, collection year, and collection locality. In total, we examined 15 adult males and 11 adult females of the

TABLE 1. Observation and illumination angles, and the resulting angle combination (α), used for color reflectance measurements taken of the plumage of Swallow Tanagers.

Observation angle (β)	Illumination angle (ω)	α (|β − ω|)
25°	25°	0°
25°	45°	$20°_a$
135°	155°	$20°_b$
25°	70°	$45°_a$
45°	90°	$45°_b$
25°	90°	$65°_a$
90°	155°	$65°_b$
25°	115°	90°
25°	155°	130°

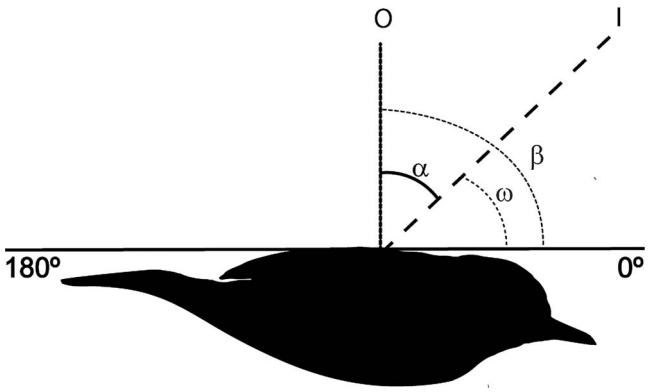

FIGURE 1. Schematic representation of the setup used to measure plumage reflectance spectra of Swallow Tanager museum skins with different angle combinations. "I" represents the orientation of the illuminant probe from which the plumage was illuminated, and "ω" is the angle formed between "I" and the museum skin's longitudinal axis. "O" represents the observational direction from which the reflected light was collected, and "β" is the angle formed between "O" and the museum skin's longitudinal axis. The angle formed between I and O is represented by α.

subspecies *Tersina viridis viridis* (Appendix Table 2). Subspecific differences in plumage color have not been reported for males, but females of the race *T. v. grisescens* have been described as grayer than females of the nominate subspecies (Hilty 2011). We specifically excluded from the study individuals with mixed green and blue plumage coloration typical of juvenile Swallow Tanagers (Schaefer 1953).

Reflectance Spectrophotometry

We measured plumage reflectance spectra with an Ocean Optics USB2000 spectrophotometer with a PX-2 pulsed xenon light source (with an emission range from 220 to 750 nm) calibrated against a WS-1 diffuse reflectance standard (Ocean Optics, Dunedin, Florida, USA) as a white standard and with the light source off (permitting no external light to enter) as a dark standard. The spectrophotometer resolution was 0.35 nm, and each spectrum was the average of 10 readings with an integration time of 100 msec. We used a boxcar smoothing function of 10.

We used 2 different probes, 1 connected to the light source for illuminating the plumage and 1 connected to the spectrophotometer to collect the reflectance data. We constructed 2 probe holders of epoxy resin with several probe entrances at fixed angles, and covered them (both internally and externally) with black matte paint to avoid light reflection within the probe holder. This allowed us to collect reflectance spectra at a fixed distance from the plumage surface, isolated from ambient light, and with 9 different angle combinations (Table 1, Figure 1). Structural noniridescent plumage color hues depend on the observer's position relative to the light source and, to a much lesser extent, on the orientation of the feather (Osorio and Ham 2002, Noh et al. 2010); thus, we determined the angle formed between the illumination and collection probes (α; Table 1, Figure 1). This included angle combinations that produced the same values of α but with different observation and illumination angles (Table 1). We expected less variation in color between angle combinations with the same α values (e.g., 20_a and 20_b in Table 1) than between those with different α values. We recalibrated the equipment before measuring the plumage reflectance of each individual and for each angle combination. The angle combination that resulted in $\alpha = 0°$ was obtained with a single bifurcated probe that illuminated the plumage and collected the reflected light simultaneously.

We measured reflectance spectra once from 4 plumage patches (head, back, rump, and chest) on each sex and then averaged measurements for each individual and α. We selected these plumage patches because they appeared homogeneously colored, were large enough to allow accurate measurements, and were all blue in males and all green in females. These 4 plumage patches showed similar values for color descriptors for all angle combinations (Appendix Figure 7), and have previously been shown to have similar reflectance patterns (Barreira et al. 2008); therefore, we averaged them to obtain a single reflectance spectrum per individual, representative of this species' overall blue and green coloration. We averaged the reflectance data in 1 nm bins for both the sexual dichromatism and conspicuousness analyses (see below).

Color descriptors. ΔS values, estimated from the Vorobyev–Osorio avian visual model, are a measure of color differences as would be perceived by a bird (Vorobyev and Osorio 1998; see below) and are, therefore, the most biologically meaningful descriptors of color differences. However, these are not easy to interpret relative to the specific aspects of plumage coloration that determine such perceptual differences. Therefore, we also compared traditional color descriptors (Montgomerie

2006) between sexes for each of the angle combinations employed. We estimated: (1) hue as the wavelength of maximum reflectance ($\lambda_{R\max}$); (2) average brightness (AvBr) as the sum of reflectance values over the entire range of wavelengths divided by the number of datapoints in the reflectance spectrum ($\Sigma R_{300-700\ nm}$ / 1152); (3) chroma, a measure of the color's spectral saturation, as the difference between the maximum and minimum reflectance values divided by average brightness (($R_{max} - R_{min}$) / AvBr); and (4) UV chroma, an index of the proportion of UV light reflected in relation to overall reflectance that describes color variation within a range of wavelengths to which humans are blind, as the ratio between the sum of reflectance between 300 and 400 nm and the sum of reflectance over the entire spectrum of wavelengths to which birds are sensitive ($\Sigma R_{300-400\ nm}$ / $\Sigma R_{300-700\ nm}$). We estimated these 4 parameters for each plumage patch and averaged them for each individual and α value.

Sexual dichromatism. To assess how sexual dichromatism in this species varies with viewing geometry from an avian perspective, we compared plumage coloration between and within sexes for each angle combination using the Vorobyev–Osorio color discrimination visual model (Vorobyev and Osorio 1998), implemented in the SPEC package (Hadfield 2004) for R 1.6.2 (R Core Team 2013). The Vorobyev–Osorio model allows the calculation of Δ*S*, which is a measure of color difference as would be perceived by a bird between 2 color points described by their reflectance spectra, considering only the chromatic component of color (i.e. independent of brightness, but dependent on the shape of the reflectance spectra). Δ*S* is a function of the sensitivities of the visual cones and their relative abundance in the retina, the reflectance spectra, the irradiance spectrum, and the transmission of the ocular media (Vorobyev and Osorio 1998, Vorobyev et al. 1998). Δ*S* is measured in units of "just noticeable difference" (jnd), with the discrimination threshold located between 1.0 and 2.0 jnd depending on the intensity of the illuminant (Eaton 2005, Burns and Shultz 2012). The spectral sensitivities and abundances of the different visual cones in the Swallow Tanager have not yet been described; therefore, we used those of the Blue Tit (*Cyanistes caeruleus*; Hart et al. 2000) as proxies in all analyses. There are 2 major classes of avian visual system defined by the spectral tuning of the most shortwave-sensitive single cones (Ödeen et al. 2011). The Blue Tit has an ultraviolet-sensitive (UVS) type of color vision system, which means that the spectral sensitivity of its shortwave-sensitive single cone is in the UV range (355–380 nm; Ödeen et al. 2011). It is likely that the vision system of the Swallow Tanager also is of the UVS avian color vision type because its close relative, the Red-legged Honeycreeper (*Cyanerpes cyaneus*; Barker et al. 2015), possesses UV-sensitive cones (Ödeen and Håstad 2010). We used ocular media and cone ratio data for the Blue Tit for our calculations of Δ*S*. We did not include irradiance in our analysis, because if color constancy correction mechanisms are accounted for when estimating avian color discrimination, then ambient light has a negligible effect on the results (Stoddard and Prum 2008, Delhey and Peters 2008).

Conspicuousness. To test for changes in plumage conspicuousness with viewing geometry in the Swallow Tanager, we calculated the Δ*S* between plumage color and the reflectance spectrum of the canopy of deciduous forest trees obtained from the ASTER spectral library of NASA (http://speclib.jpl.nasa.gov; Baldridge et al. 2009) as a representative of a plausible background habitat for this species (Schaefer 1953); thus, the contrast between the color of Swallow Tanagers' plumage patches and the surrounding vegetation as would be perceived by an avian observer served as a proxy of color conspicuousness (Håstad et al. 2005). We estimated Δ*S* as above using the cone sensitivities of Blue Tits as representative of a UVS type of visual system (such as that of most passerines; Ödeen et al. 2011), and those of the Red Junglefowl (*Gallus gallus*; Govardovskii and Zueva 1977, Partridge 1989, Bowmaker et al. 1997) as representative of the violet-sensitive (VS) type of color vision thought to be typical of falconiiforms (falcons, hawks, and their allies; Ödeen and Håstad 2013, Lind et al. 2013), the most likely avian predators of Swallow Tanagers (Schaefer 1953).

Statistical Analyses

As our data for color descriptors did not meet the assumption of normality, we performed Mann-Whitney *U*-tests to compare the 4 color descriptors between sexes for each angle combination. We performed paired *t*-tests to evaluate differences between the Δ*S* values obtained as measures of conspicuousness for UVS and VS birds for each angle combination. We performed all statistical analyses with SPSS 15.0 for Windows (SPSS, Chicago, Illinois, USA). Reported values are expressed as means ± SD.

RESULTS

Color Descriptors

Average brightness showed significant intersexual differences, with males reflecting more light than females for all angle combinations (all $U > -4.28$, all $P < 0.001$; Figure 2, Figure 3A) except $\alpha = 130°$ ($P = 0.11$). We found no difference between the sexes in hue at $\alpha = 0°$ ($P = 0.12$), where peak reflectance was located in green wavelengths for both sexes (Figure 2, Figure 3B), but we found significant differences for all other angle combinations (all $P < 0.01$). For males, peak reflectance shifted toward blue–violet wavelengths with increasing α, while for females, peak reflectance was located in green–yellow

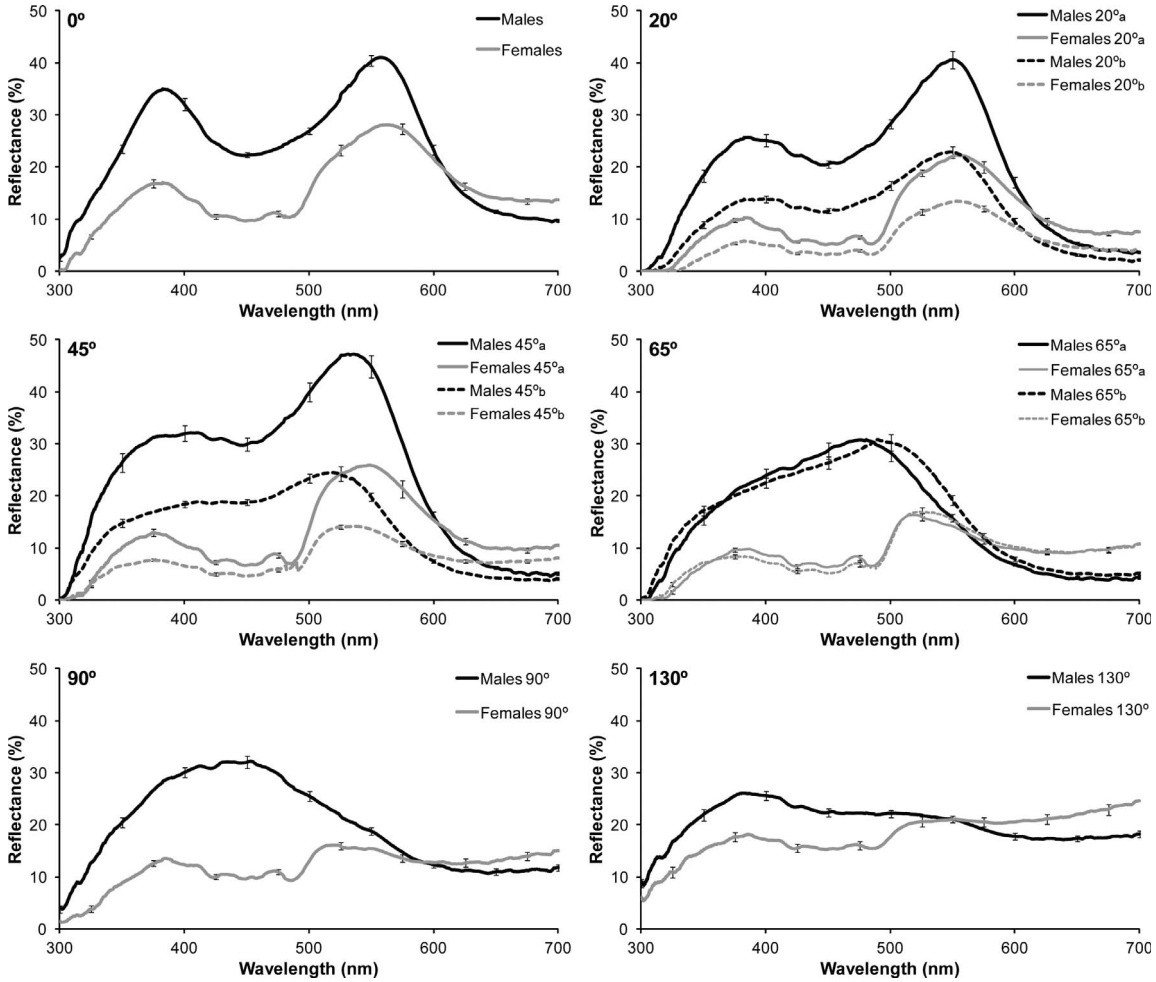

FIGURE 2. Mean reflectance spectra (± SE) of male and female Swallow Tanager plumages for 9 different angle combinations (α, defined in Figure 1). Each spectrum is the result of averaging the plumage reflectance of the head, chest, back, and rump. For the α values of 20°, 45°, and 65°, we had 2 different combinations of illuminating and collecting angles (indicated with the suffixes a and b; see Table 1), and both reflectance spectra are shown for each sex in the same panel.

wavelengths for all angle combinations (Figure 2, Figure 3B). The chroma values for female plumage were significantly greater than those for male plumage for α ranging from 0° to 45°, inclusive (all $P < 0.002$; Figure 3C), but were not significantly different between the sexes for α values between 65° and 90° (all $P > 0.05$). This is probably due to a secondary reflectance peak in UV wavelengths for male plumage when illumination and observation angles were similar, while the secondary and main reflectance peaks merged as α increased (Figure 2). Female chroma was also significantly greater than male chroma at $\alpha = 130°$ ($P = 0.005$), but this angle combination produced the least saturated reflectance measurement for both sexes (Figure 2, Figure 3C). Finally, we found significant sexual dichromatism in UV chroma for all α values (all $P < 0.001$), with males reflecting a larger proportion of UV light than females in all cases (Figure 2, Figure 3D). Although male and female mean values varied at different α, UV chroma values showed similar differences in magnitude between the sexes for all angle combinations (Figure 3D). Therefore, of the 4 color descriptors used here, UV chroma was the most reliable for characterizing intersexual differences in this species, independent of viewing geometry.

Sexual Dichromatism

In all cases, except for the intrasexual comparisons of plumage color obtained with $\alpha = 130°$, ΔS values were above the 1 jnd discrimination threshold. This means that the color differences both between and within sexes should be perceivable by UVS birds under good lighting conditions (Figure 4A, 4B). However, the intersexual comparisons produced values of ΔS that were between 2.8 and 5.1 times higher than the intrasexual comparisons

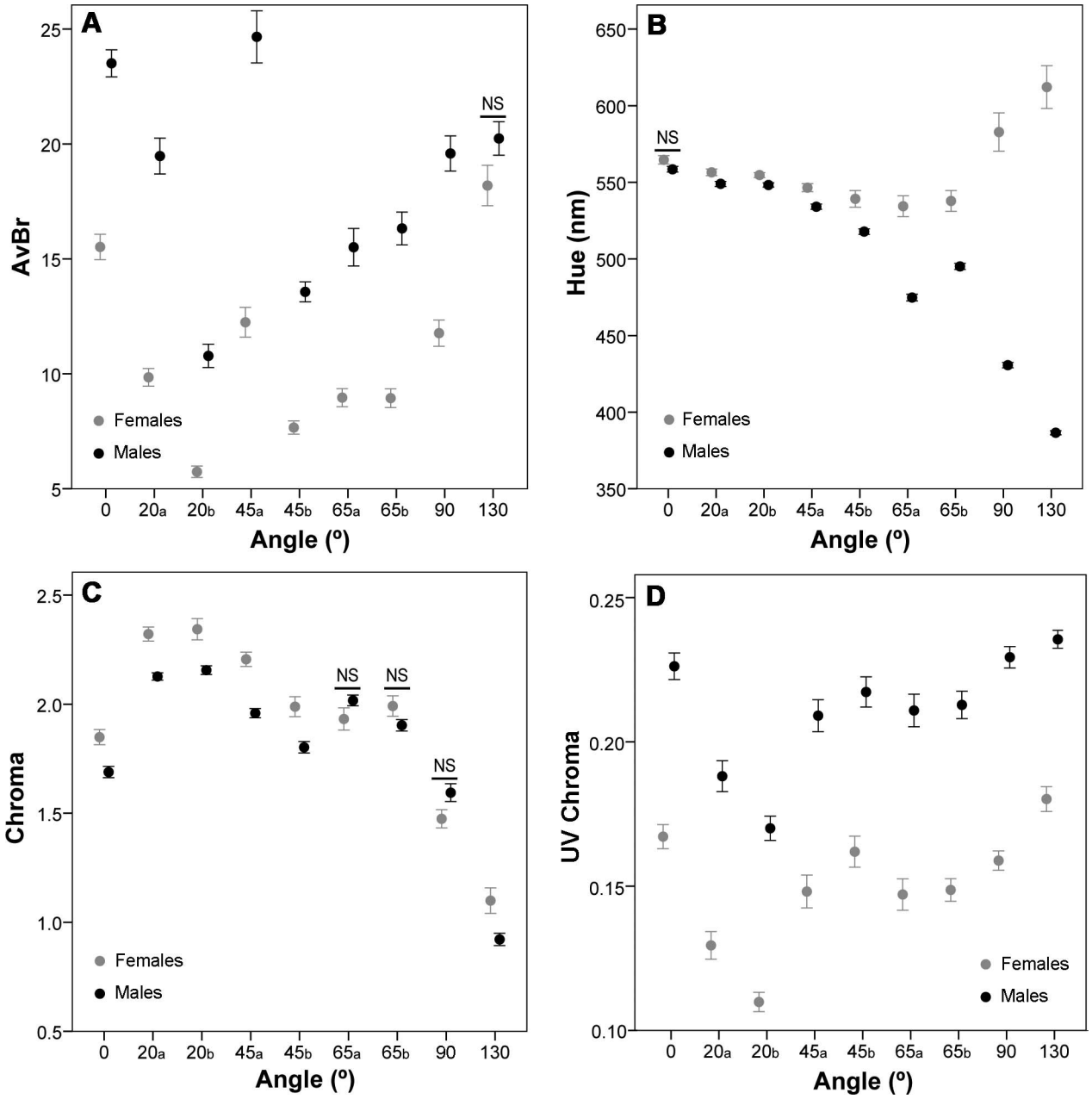

FIGURE 3. Mean scores (± SE) for plumage color descriptors for male and female Swallow Tanagers for 9 different angle combinations (α, defined in Figure 1). For the α values of 20°, 45°, and 65°, we had 2 different combinations of illuminating and collecting angles (indicated with the suffixes a and b; see Table 1). (**A**) Average brightness (AvBr), estimated as the average percent reflectance across all wavelengths measured; (**B**) Hue, estimated as the wavelength of maximum reflectance; (**C**) Chroma, a measure of color saturation; and (**D**) UV Chroma, the proportion of UV light reflected in relation to total reflectance. NS indicates nonsignificant intersexual differences.

at each α, with ΔS increasing with α to a maximum at $\alpha = 65°$, and then decreasing to a minimum at $\alpha = 130°$ (Figure 4A). In comparison, the values of ΔS for intrasexual comparisons were fairly constant for the different α (Figure 4B). As expected, the ΔS values obtained for measurements made with equal values of α ($20°_a$ and $20°_b$, $45°_a$ and $45°_b$, and $65°_a$ and $65°_b$; Table 1) were similar.

Conspicuousness

We obtained values of ΔS larger than 1 jnd for all comparisons of plumage coloration with the foliage of deciduous trees at all angles for both males and females, and for both UVS and VS visual systems (Figure 4C, 4D). However, the contrast between the plumage coloration of males and the background foliage varied markedly for the

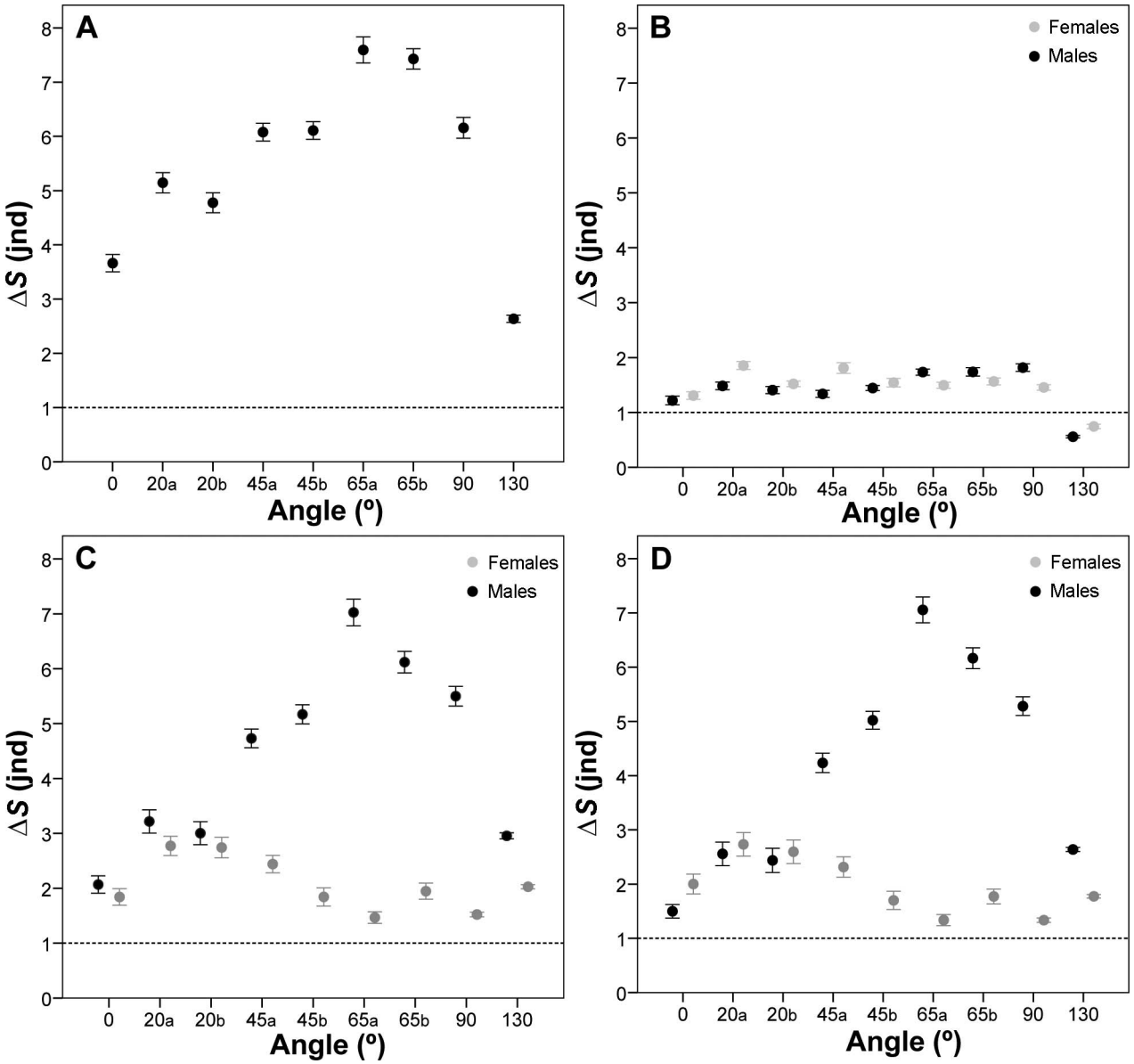

FIGURE 4. Mean ΔS (a measure of color difference as would be perceived by a bird following the Vorobyev–Osorio avian visual model; Vorobyev and Osorio 1998) values (± SE) in the Swallow Tanager obtained for different angle combinations (α, defined in Figure 1). The dotted line shows the 1 jnd (just noticeable difference) color discrimination threshold. (**A**) Levels of sexual dichromatism measured as ΔS between the plumage coloration of each sex; (**B**) levels of intrasexual variation in plumage color measured as ΔS, by sex; (**C**) conspicuousness, measured as ΔS between plumage coloration and the reflectance spectrum of the canopy of deciduous trees as seen by a UVS (ultraviolet-sensitive, the color vision system of a conspecific) bird, by sex; and (**D**) conspicuousness, measured as ΔS between plumage coloration and the reflectance spectrum of the canopy of deciduous trees as seen by a VS (violet-sensitive, the color vision system of a potential avian predator) bird, by sex.

different α, being lowest when the light source and observer were oriented in the same direction ($\alpha = 0°$) and highest when they formed an angle of 65°. The conspicuousness of females against the background was similar to that of males at low angles between the light source and the observer ($\alpha = 0°$ and $\alpha = 20°$), but decreased slightly at higher values of α. Male plumage was less conspicuous to the VS visual system for all angle combinations, with all contrasts being significant (all $t_{14} > 4.4$, all $P < 0.001$) except those for both $\alpha = 65°$ (both $t_{14} < -1.4$, both $P > 0.20$). The difference in conspicuousness of males between the 2 visual systems (between 0.56 and 0.67 jnd; Figure 4C, 4D) was larger when the illumination and observation angles were similar ($\alpha = 0°$ and $\alpha = 20°$). According to this result, the plumage of males was 23%–38% more conspicuous to the eyes of conspecifics than to

the eyes of potential avian predators for these angle combinations. The value of this percentage difference of ΔS between visual systems cannot be interpreted as being the same as the Vorovyev–Osorio visual model's perceptual threshold of 1 jnd because that threshold applies to the comparison of 2 colors within a given visual system. However, similar ΔS values have been considered biologically significant in past studies (Håstad et al. 2005).

The conspicuousness of females was similar across visual systems, but significantly larger for the VS visual system at $\alpha = 0°$ ($t_{10} = -3.24$, $P = 0.005$; Figure 4C, 4D), and significantly and slightly larger for the UVS visual system for all other values of α (all $t_{10} > 3.21$, all $P < 0.009$; Figure 4C, 4D) except $\alpha = 20°_a$ ($t_{10} = -0.88$, $P = 0.40$).

DISCUSSION

Using objective methods of color quantification, we found marked variation in the sexual dichromatism and conspicuousness of male Swallow Tanagers in relation to viewing geometry. These findings were related to changes in the shape of reflectance spectra due to the relative positions of the light source and the observer, resulting in fluctuations in hue and chroma in male plumage. Notably, the angle combination that produced the maximum sexual dichromatism was also that which produced the highest male conspicuousness but the highest female crypsis. Plumage coloration is often thought to evolve in response to opposing selective pressures, with sexual selection acting more strongly on males to produce more conspicuous colors, but natural selection favoring crypsis to reduce predation risk (Burns 1998, Gomez and Théry 2007, Olsen et al. 2010, Dunn et al. 2015). However, the pattern of color change with viewing geometry that we found in male Swallow Tanagers suggests that the same plumage coloration can increase and/or decrease exposure according to viewing conditions, which individuals could optimize by selecting specific lighting environments (Dakin and Montgomerie 2009, Sicsú et al. 2013).

Burns and Shultz (2012) found that the blue-green tanager clade (which includes the Swallow Tanager) was the most sexually dichromatic within the tanagers. However, in their study, the authors used only a single probe that collected light and illuminated plumage simultaneously (equivalent to our $\alpha = 0°$, where we obtained one of the smallest values of sexual dichromatism, with both sexes reflecting maximally at green wavelengths). We assert that sexual dichromatism in this species is probably much higher than previously noted because we found that male plumage reflected maximally within the blue range, with a single reflectance peak at $\alpha = 65°$, while females had a green hue. Plumage coloration with high reflectance of short wavelengths is the most efficient for increasing conspicuousness within canopy birds, while green plumage coloration is optimal for maximizing crypsis (Gomez and Théry 2004).

The change in conspicuousness of males with viewing geometry followed the same pattern as sexual dichromatism, with minor contrast between males and the background obtained for small angles between the viewer and light source and maximum contrast at a 65° angle. Our results imply that male plumage will be less conspicuous to the eyes of avian predators, which have a VS type of color vision, than to conspecifics, which have a UVS type of color vision, for almost all of the angle combinations measured. This is consistent with the results of Håstad et al. (2005), who found similar differences in conspicuousness between visual systems for the coloration of several passerine species; this is probably related to the high UV reflectance in the spectra of males. Concordantly with our results, Lind and Delhey (2015) determined that the plumage coloration of the Swallow Tanager (among other species) is better suited to detection by the UVS type of vision, producing a higher contrast gain compared with the VS type of color vision, although this study did not investigate color variation with viewing geometry.

The values of ΔS that we obtained were almost always higher than the 1 jnd threshold of visual discrimination for optimal lighting conditions (and also higher than the more conservative value of 2 jnd), even for intrasexual comparisons of plumage coloration. This implies that birds are capable of discerning color differences even among individuals of the same sex. Previous studies also have obtained high values of ΔS within groups, suggesting that color discrimination among individuals might be more pervasive than previously thought (Delhey and Peters 2008, Cornuault et al. 2015). Sexually selected traits are expected to show greater interindividual variation, as they can serve to assess individual quality; for instance, Delhey and Peters (2008) determined that plumage coloration was more variable in plumage patches suggested to have a sexual signaling function and/or condition-dependent coloration. Past studies that have assessed the extent of color differences between the sexes or among species usually have only estimated the average ΔS between the groups of interest and have not quantified variation in color perception within these groups (Eaton 2005, Burns and Schultz 2012). Thus, intragroup variation has been largely overlooked in many studies employing avian visual models, despite the fact that sexual dichromatism is frequently considered an indicator of sexual selection (but see Delhey and Peters 2008). Additionally, differences in coloration among females can be as high as those among males, suggesting that individual assessment through plumage color can be important in both sexes (Delhey and Peters 2008).

Sun location plays a key role in determining courtship rate and body orientation in male birds with iridescent

coloration (Dakin and Montgomerie 2009, Sicsú et al. 2013), which affects their reproductive success (Dakin and Montgomerie 2013). Observations of Swallow Tanager reproductive behavior suggest an important role of visual communication and the selection of lighting conditions by displaying individuals (Schaefer 1953). Swallow Tanagers inhabit mainly the canopy and open areas and are active mostly during early morning and afternoon, which indicates that they are seemingly sensitive to changes in light intensity (Schaefer 1953). Males select high branches to perform complex sexual displays during mate selection, and plumage color seems to play a role in both intra- and intersexual interactions (Schaefer 1953). Our findings suggest that striking variation in sexual dichromatism and conspicuousness likely affects displays and exposure to potential avian predators in this species (and probably others with the same double scattering phenomenon). We can make specific predictions, for future researchers to test, regarding the relative positions of a male Swallow Tanager, the sun, and a third interacting individual in situations in which increased or decreased conspicuousness and sexual dichromatism will be beneficial. For example, against dominantly green backgrounds, males should prefer to position themselves between the light source and the observer during sexual interactions (α values of 65° to 90°), but facing both the light source and the observer when exposed to predators (α values from 0° to 20°). Alternatively, this sort of plumage coloration could simply be a by-product of the generation of structural colors with specific hues that results in the production of a secondary reflectance peak due to double scattering (Noh et al. 2010, Saranathan et al. 2012). It is necessary to perform behavioral tests on species showing this kind of plumage coloration to discern between these 2 possibilities (biological signaling function vs. a by-product of structural color production mechanisms).

Few studies of avian coloration have considered variation in color in noniridescent plumage coloration resulting from changes in viewing geometry (Osorio and Ham 2002, Santos et al. 2007). This is, to the best of our knowledge, the first study to document a substantial change with viewing geometry in sexual dichromatism and conspicuousness in noniridescent plumage coloration from an avian perspective. Overall, our results highlight the need to consider viewing geometry when trying to gain an understanding of the use of visual signals in avian communication, particularly for plumage coloration such as that found in the Swallow Tanager, otherwise sexual dichromatism and conspicuousness may be over- or underestimated. It is particularly important for researchers studying the plumage coloration of species with described double scattering to consider viewing geometry in order to quantify plumage reflectance in a biologically meaningful manner. For species for which this phenomenon has not been described, but that possess structural coloration, a visual inspection employing varying angles of observation and illumination could provide an approximate idea of the presence of a similar effect (Appendix Figures 5 and 6). Unlike what occurs with iridescent colors, the position of the feather relative to the observer and/or the light source does not qualitatively change the results for the coloration pattern described here. However, the use of a goniometer to fix illuminant and observer angles (such as those employed by studies of iridescent coloration) would help to improve the repeatability and standardization of color measurements across studies (Meadows et al. 2011, Van Wijk et al. 2016). Appropriate color descriptions, together with more knowledge about the visual context during the occurrence of sexual displays or signaling in the Swallow Tanager, will be crucial to understanding the functionality of structural plumage coloration with double scattering.

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Author contributions: A.S.B., N.C.G., P.L.T., and S.C.L. conceived the idea, design, and experiment (supervised research, formulated question or hypothesis). A.S.B. and N.C.G. performed the experiments (collected data, conducted the research). A.S.B. wrote the paper and analyzed the data. P.L.T. and S.C.L. contributed substantial materials, resources, or funding.

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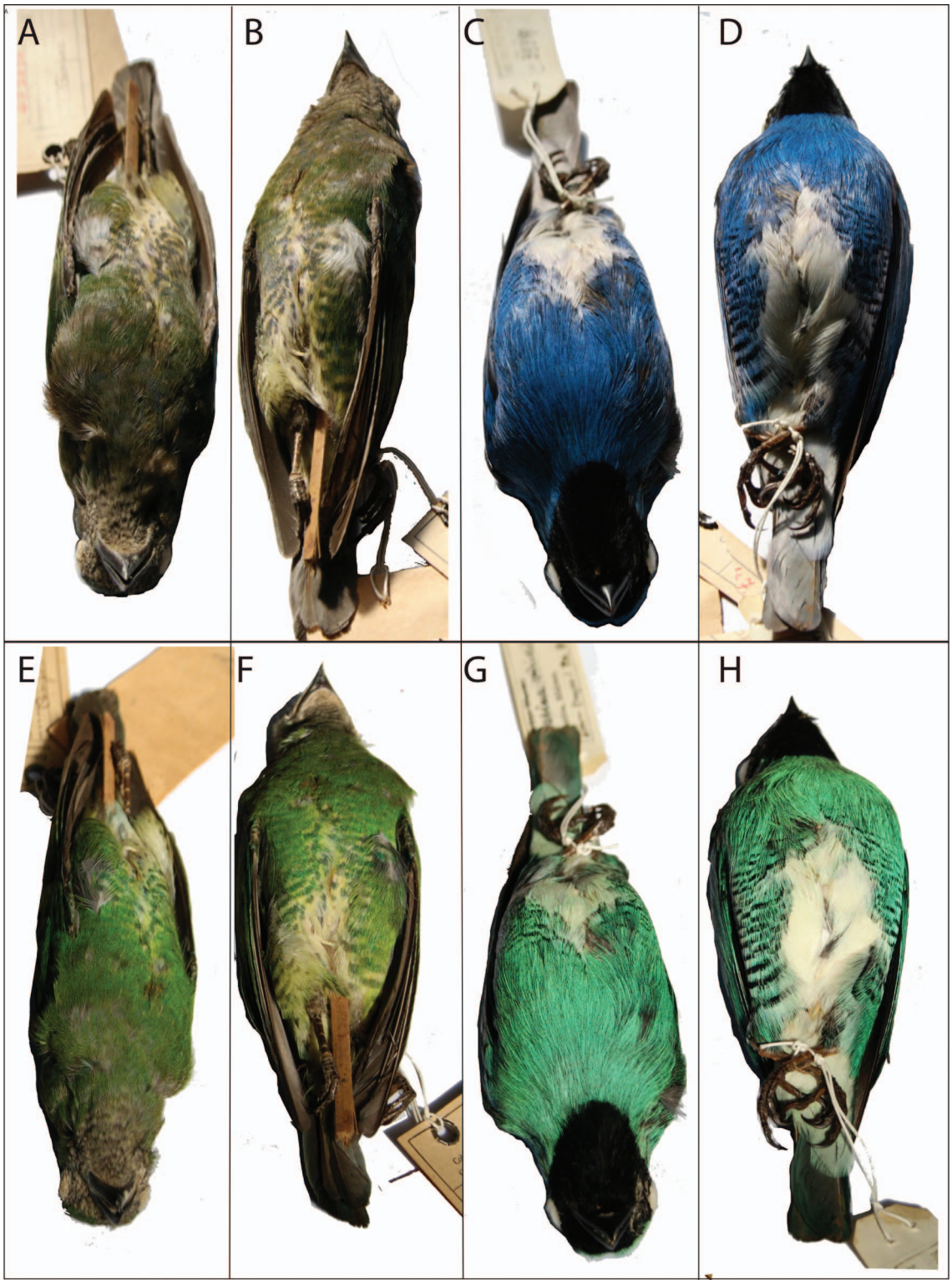
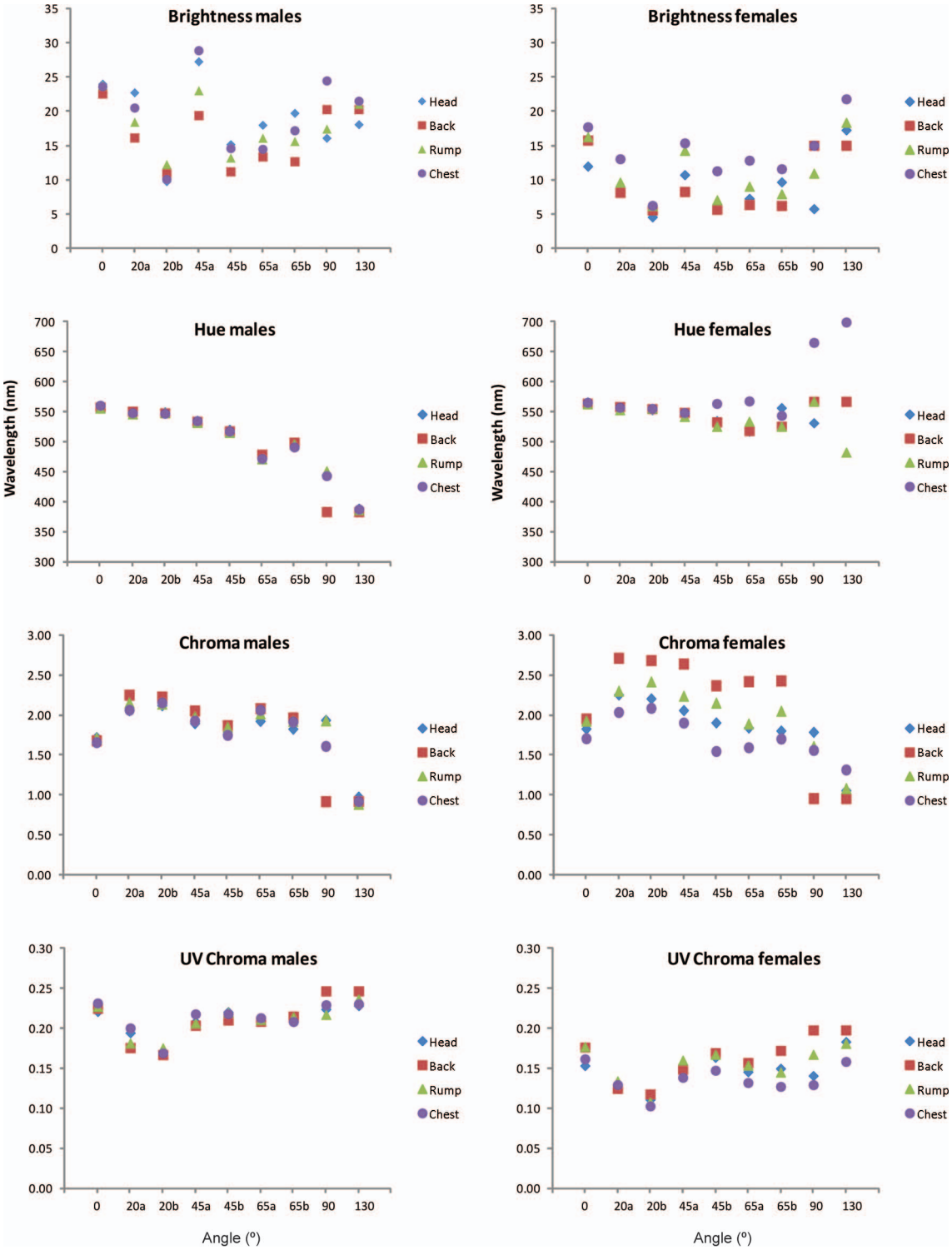
APPENDIX TABLE 2. Detailed list of the study skins of Swallow Tanagers (*Tersina viridis*) deposited in the ornithology collection of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" employed for color reflectance measurements.

Sex	Collection code	Collection date	Collection locality
Male	MACN-Or 33286	September 25, 1951	Arroyo Urugua-í km 10, Misiones, Argentina
Male	MACN-Or 43432	September 18, 1960	Arroyo Urugua-í km 30, Misiones, Argentina
Male	MACN-Or 34542	October 31, 1953	Tobuna, Dpto. Frontera, Misiones, Argentina
Male	MACN-Or 33284	September 12, 1951	Arroyo Urugua-í km 10, Misiones, Argentina
Male	MACN-Or 37272	November 25, 1954	Refugio Piñalitos, Dpto. Frontera, Misiones, Argentina
Male	MACN-Or 39719	October 2, 1959	Arroyo Urugua-í km 10, Misiones, Argentina
Male	MACN-Or 37269	October 3, 1954	Arroyo Urugua-í km 30, Misiones, Argentina
Male	MACN-Or 37268	October 3, 1954	Arroyo Urugua-í km 30, Misiones, Argentina
Male	MACN-Or 43041	November 14, 1966	Floresta da Tijuca, Rio de Janeiro, Brazil
Male	MACN-Or 45732	December 18, 1958	Arroyo Urugua-í km 10, Misiones, Argentina
Male	MACN-Or 3947a	October 8, 1933	Corpus, Misiones, Argentina
Male	MACN-Or-37271	November 25, 1954	Refugio Piñalitos, Dpto. Frontera, Misiones, Argentina
Male	MACN-Or 37267	September 8, 1954	Arroyo Urugua-í km 30, Misiones, Argentina
Male	MACN-Or 71117	November 29, 2007	PN Iguazú, Misiones, Argentina
Male	MACN-Or 71104	November 27, 2007	PN Iguazú, Misiones, Argentina
Female	MACN-Or 39720	October 2, 1959	Arroyo Urugua-í km 10, Misiones, Argentina
Female	MACN-Or 37270	October 13, 1954	Arroyo Urugua-í km30, Misiones, Argentina
Female	MACN-Or 39789	December 28, 1958	Arroyo Urugua-í km 10, Misiones, Argentina
Female	MACN-Or 34539	October 25, 1953	Tobuna, Dpto. Frontera, Misiones, Argentina
Female	MACN-Or 33909	September 17, 1952	Arroyo Urugua-í km 10, Misiones, Argentina
Female	MACN-Or 39792	1959	Arroyo Urugua-í km 10, Misiones, Argentina
Female	MACN-Or 39791	1959	Arroyo Urugua-í km 10, Misiones, Argentina
Female	MACN-Or 39790	1959	Arroyo Urugua-í km 10, Misiones, Argentina
Female	MACN-Or 47336	December 12, 1938	Capitán Meza, Alto Paraná, Paraguay
Female	MACN-Or 3851a	May 1934	Santa Ana, Misiones, Argentina
Female	MACN-Or 71104	November 27, 2007	PN Iguazú, Misiones, Argentina



APPENDIX FIGURE 5. Images of female (A, B, E, F) and male (C, D, G, H) Swallow Tanager study skins taken under natural lighting conditions (without flash). A–D were taken with the light source located in front of the camera, and E–H were taken with the light source located behind the camera. Images A–B, C–D, E–F, and G–H show the same individual under the same lighting conditions but in a different position, to illustrate that the perceived color change does not depend on feather orientation.

APPENDIX FIGURE 6. Images of study skins of species of Thraupidae other than Swallow Tanagers with reported double scattering (Saranathan et al. 2012), taken under natural lighting conditions (without flash). A–E were taken with the light source located in front of the camera, and F–J were taken with the light source located behind the camera. A and F show *Tangara ruficervix*; B and G show *Tangara cyanicollis*; C and H are of *Thraupis episcopus*; D and I are of *Dacnis cayana*; and E and J show *Dacnis lineata*.



APPENDIX FIGURE 7. Average color descriptors (brightness, hue, chroma, and UV chroma) for each plumage patch (head, back, rump, and chest) of Swallow Tanager study skins by sex for each angle combination measured (see Table 1).