Letters

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Analysis from avian visual perspective reveals plumage colour differences among females of Capuchino Seedeaters (*Sporophila*)

Pilar Benites, Muir D. Eaton, Darío A. Lijtmaer, Stephen C. Lougheed and Pablo L. Tubaro

P. Benites, D. A. Lijtmaer, and P. L. Tubaro, División Ornitología, Museo Argentino de Ciencias Naturales ¨Bernardino Rivadavia¨, Angel Gallardo 470, CABA (C1405DJR), Argentina. – M. D. Eaton (muir.eaton@drake.edu), Biology Dept, Drake Univ, Des Moines, Iowa, USA. – S. C. Lougheed, Dept of Biology, Queen's Univ, Kingston, Ontario, Canada.

Females of the closely related capuchino seedeaters are difficult to distinguish from one another based on human visual perception of colouration and morphology. We examined plumage colour differences among females of four species, the tawny-bellied seedeater *Sporophila hypoxantha*, the dark-throated seedeater *S. ruficollis*, the rufous-rumped seedeater *S. hypochroma*, and the chesnut-bellied seedeater *S. cinnamomea*. Reflectance values were measured on museum skins, and interspecific differences were analyzed using the Vorobyev-Osorio avian colour discrimination model. Interspecific distances in the colour space calculated by the model were considerably higher than the threshold for colour discrimination, indicating the presence of colour differences among species that should be detectable by birds. Colour differences between *S. hypoxantha* and the other three species were the largest. A Discriminant Function Analysis showed that UV-wavelength was particularly important in species separation. Our results indicate that female plumage of these four species is considerably divergent in colour; these differences being imperceptible to the human eye, thus representing previously unknown morphological evolution in these species.

Speciation is a central topic in evolutionary biology, and many studies have focused on the mechanisms by which species are reproductively isolated. Visual signals used in species recognition and sexual selection are considered to be among the most important prezygotic barriers to reproduction (Coyne and Orr 2004). Many studies have sought to explain the adaptive significance of interspecific variation in avian plumage colouration (Darwin 1871, Mayr 1942, Andersson 1994), with the traditional explanation being that it helps to minimize the risk of hybridization by serving as species recognition signals (Dobzhansky 1940, Mayr 1942). This is particularly important for morphologically similar and closely related species living in sympatry, where the chances of hybridization are high (Miller 1982).

The Neotropical genus *Sporophila* consists of ca 30 species of small (10–12.5 cm) granivorous birds with strong bills that inhabit open and semi-open areas from the southern United States to southern South America (Meyer de Schauensee 1952, Ridgley and Tudor 1989). Species in the genus have marked sexual plumage dimorphism, with males typically being colourful (though not brilliant) and boldly patterned and females dull coloured and extremely similar across all species (Ridgley and Tudor 1989). The capuchinos comprise a monophyletic group of 11 species within the genus (Lijtmaer et al. 2004), and some of these occur in sympatry. This group has undergone a recent and explosive radiation, and its phylogenetic relationships and the taxonomic status of some of its species remain unresolved (Lijtmaer et al. 2004). Species in this group vary little in morphology and size, but the cinnamon-based plumage colouration of males is fairly distinctive among species, mainly due to the presence or absence of white, black and grey patches of colour (Ridgely and Tudor 1989). In contrast, the drab female plumage of the capuchinos makes species identification very difficult even with the bird in hand (Ridgley and Tudor 1989, Ouellet 1992).

Signals can only be understood with reference to the natural receiver (Endler 1992), and the striking differences in visual systems and colour perception between human and birds make human description of plumage colour inadequate for the study of many biological questions (Bennett et al. 1994, Bowmaker et al. 1997). Using reflectance spectrometry and the avian visual model of Vorobyev and Osorio (1998), and a Discrimant Function Analysis, we tested for colour differences in plumage that are visually cryptic to humans yet potentially visually discernable to birds among females of four capuchino species, the tawny-bellied seedeater *Sporophila hypoxantha*, the dark-throated seedeater *S. ruficollis*, the rufous-rumped seedeater *S. hypochroma*, and the chestnut- bellied seedeater *S. cinnamomea*. These four southern South American species are sympatric in northeastern Argentina and southeastern Paraguay, and thus interspecific colour differences identified by the avian visual models represent potential visual signals for, say, species recognition, and in the least, previously unrecognized morphological evolution among

these species. Furthermore, to our knowledge, this is the first application of an avian visual model to study interspecific variation in female plumage colouration.

Materials and methods

Data collection

We used museum study skins from the Museo Argentino de Ciencias Naturales ''Bernardino Rivadavia''. Only female specimens that have been unequivocally sexed based on their gonads during skin preparation, and that were in perfect condition with full information about species and locality were used, totaling nine *S. hypoxantha*, six *S. hypochroma*, six *S. cinnamomea* and 16 *S. ruficollis*. Although female capuchinos are difficult to assign to species based on plumage, we are confident in the identification of the museum specimens used in this study because, either: 1) a male skin with the same date of collection and locality was associated with the female skin, suggesting that both specimens were collected together, or 2) the female was collected in a locality where only one species of capuchino is known to occur.

All specimens were from locations along the Parana-Paraguay Rivers basin, with the exception of six of the 16 *S. ruficollis* females that were collected in Tucumán (5 specimens) and the Bolivian-Argentinan border (1 specimen). The collection dates of the individuals ranged from 1903 to 1998 (average collection year $\pm$ SD for *S. hypoxantha* = 1974 $\pm$ 25, for *S. hypochroma* = 1996 $\pm$ 3, for *S. cinnamomea* = 1991 $\pm$ 11, and for *S. ruficollis* = 1925 $\pm$ 22). We measured plumage colouration on seven patches that allowed at least one reflectance measurement: crown, nape, back, rump, throat, chest, and belly. Three reflectance measurements were taken from the belly and two from the back and the rump, along the midline. Only one measurement was taken from the remaining plumage regions, due to their smaller size.

We collected reflectance data using an Ocean Optics USB 2000 spectrometer (Ocean Optics Inc., Dunedin, Florida) equipped with a PX-2 pulsed xenon light source (effective emission 250–800 nm), with the following settings: average reading = 3, integrating time = 100 ms, and no boxcar smoothing. Plumage was illuminated and reflectance data (percent light reflected at each wavelength from 320 to 700 nm) were collected with the reflectance probe housed in a prismatic holder that was held (not pressed) against the chosen region on the study skin. Readings were made in an angle of 90° to the surface of the plumage region. The spectrometer was calibrated against a barium sulphate white standard prior to each individual measurement. The diameter of the circular region measured was approximately 6 mm, and the distance between the probe and the plumage was 23 mm. Readings were made blind with respect to the species of each individual specimen. Median reflectance values were extracted from 5 nm bins from 340 to 700 nm for each plumage region from each specimen and were used in subsequent data analyses. Readings below 340 nm were excluded from the study because of the considerable noise exhibited in these data. If the same plumage region was measured more than once on a specimen, individual specimen means for that plumage region were calculated prior to the extraction of median values.

Visual modeling

Colour differences among female *Sporophila* species were evaluated for each plumage region using the Vorobyev-Osorio (1998) colour discrimination model. The model calculates a distance in avian perceptual colour space (ΔS) between two colours (e.g., the spectral reflectance of plumages), defined by the quantum catches, Q_i, of each single-cone cell receptor type in the avian retina: Q_1 = UVS; UV- wavelength sensitive, Q_2 = SWS; short-wavelength sensitive, Q_3 = MWS; medium-wavelength sensitive, and Q_4 = LWS; long-wavelength sensitive, and their corresponding noise-to-signal ratios. To calculate ΔS for each interspecific plumage region comparison, we followed methods and model justifications detailed in Eaton (2005). In short, quantum catches for each single-cone cell type were calculated using spectral sensitivity function data for the blue tit *Parus caeruleus*, and noise-to-signal ratios were derived from the proportions of each of the single-cone cell types found in the blue tit retina (Hart 2001). Neither spectral sensitivity data nor cone cell type proportions are available for any of the *Sporophila* species, and thus the blue tit was used as a representative passerine UVS-visual system. Use of blue tit spectral sensitivities is largely justified, given that all passerines studied to date posses an SWS1 (short-wave sensitive) single cone maximally sensitive in the near ultra-violet wavelengths (i.e., UVS-visual system), with relatively little variation across passerines in the wavelengths of peak sensitivity for all four single cone cell types (Hart and Hunt 2007). Of the passerines, only the corvids (a clade to which *Sporophila* spp. do not belong; Barker et al. 2004) show evidence for a differing SWS1 visual sensitivity, with peak sensitivity of this single cone cell type shifted into the longer violet wavelengths (i.e., VS-visual system; Odeen and Hastad 2003). However, proportions of the single cone cell photoreceptor types have been shown to vary across passerines (Hart 2001), and these proportions define the noise-to-signal ratios that determine the distance between two colors in perceptual space (i.e.,????-please clarify S). To test the sensitivity of ???? □ [Δ???] S to different suites of cone cell type proportions, we re-calculated the colour space distance of all plumage comparisons using cone cell type proportions from European blackbird *Turdus merula* and European starling *Sturnus vulgaris*, and these two species encompass the known variation among passerines (Hart 2001). The differences among the ???? □ S values calculated with each of these photoreceptor proportion suites (i.e., blackbird, starling, blue tit), for the same plumage patch comparison, were one to two orders of magnitude smaller than the average ???? □ S value calculated using the blue tit cone proportions (data available upon request). Differences among blackbird, starling, and blue tit derived ???? □ S calculations would need to be an order of magnitude larger than a typical ????? □ S value from the blue tit derived calculations herein to alter any conclusions drawn. Thus, we present and discuss only the ????? □ S values resulting from

calculations based on cone cell type proportions from the blue tit. Similar analyses exploring the effects of different passerine cone cell proportions on colour space values found the same robust nature of ???? □ *S* calculations based on blue tit proportions (Eaton 2005, Eaton 2007).

The unit of ????? □ *S* is jnd (just noticeable difference), where 1.0 jnd is the threshold value for discrimination of two colours, and, by definition, represents a distance in perceptual colour space at which two colors would be visually discernable. Thus, ???? □ *S* values <1.0 jnd indicate differences in colour most likely not visually discernable by birds, while values >1.0 jnd indicate a magnitude of colour differentiation above the visual discriminatory abilities of birds (Vorobyev et al. 1998, Sidiqqi et al. 2004). Visual performance can vary among species and through differing viewing conditions, such as changing light environments (Vorobyev et al. 1998), but in general, at jnd $=1.0$ two colours are barely distinguishable given a set of viewing conditions, and as jnd becomes larger two colours are more rapidly discernable, even as viewing conditions change (e.g., ambient light, background reflectance, etc.) (see also Siddiqi et al. 2004). In sum, ΔS herein for a given plumage region represents the divergence in colour between *Sporophila* species with respect to the avian visual system.

Statistical analysis

The Vorobyev-Osorio model defines colour discrimination based on integration across the entire range of visual wavelengths, with no information about the contribution made by specific wavelengths to the differences found. Additionally, because average reflectance data were used in the model, differences between species identified by the model might be meaningless if the colour variation within species overlaps too greatly with the colour variation among species. Through a stepwise Discriminant Function Analysis (DFA) we analyzed interspecific variation in colour and assessed the weight of differing spectral regions in defining colour differences. A DFA predicts group membership from a set of predictors, with the four species, *S. hypoxantha*, *S. ruficollis*, *S. hypochroma*, and *S. cinnamomea*, as the grouping variable, and Q*i* (i.e. the quantum catches for the four different single-cone cell types as calculated in the visual model described above) for each plumage region as the predictor variables. In a stepwise forward DFA, the original set of predictors is reduced to a few used to calculate the discriminant functions that maximize the separation between species. Group membership predictions for each individual were compared to actual group membership through a jackknifed classification, in which individuals are omitted, in turn, when classification equations are calculated, and then the individual's group membership is tested. This procedure gives a more realistic estimate of the ability of predictors to separate groups (Tabachnick and Fidel 2001). To control for the effect of specimen age on DFA results, we performed a linear regression between the year of capture of each specimen and the predictor variables that differed the most among species. All statistical analyses were performed using SPSS 15.0 for windows package (SPSS inc.).

Results

Quantification of female plumage differences using the Vorobyev-Osorio (1998) model on the four *Sporophila* species reveals widespread colour divergence. For all plumage regions analyzed, the majority of ΔS values were much higher than the threshold for avian visual discrimination (□????S values ranged from 1.53 to 15.87 jnd; Table 1). The largest colour differences were between *S. hypoxantha* and *S. hypochroma*, and between *S. hypoxantha* and *S. cinnamomea*, with values from seven to 16 times the discrimination-threshold magnitude, depending on the plumage region. The smallest colour differences were between *S. hypochroma* and *S. cinnamomea*, and *S. cinnamomea* and *S. ruficollis*, although most plumage regions compared between these species still exceeded the discrimination-threshold by two to six times. The plumage region that showed the highest values of???? □ *S* is the crown, followed by the rump, throat, and back. The chest and belly had the lowest values, while the nape exhibited intermediate values (Table 1).

In the stepwise DFA, Q1 and Q2 from crown and back, and Q4 from belly were the predictors that maximized differences between species and the ones used to calculate the discriminant functions and classification equations. Three discriminant functions were calculated, with $\chi^2 = 119.78$, $p < 0.001$. After removal of the first function, there was still a strong association between groups and predictors, $\chi^2 = 24.58$, $p < 0.005$, but when first and second discriminant functions were removed, there was no significant association between groups and predictors ($\chi^2 = 4.79$, $p = 0.188$). The first and second functions accounted for 95% and 4.3%, respectively, of the between group variability. As shown in Fig. 1, the first discriminant function clearly separates the four species, while in the

Table 1. Colour differentiation (□ ????*S*) between females of *S. hypoxantha, S. ruficollis, S. hypochroma,* and *S. cinnamomea.* □?????*S* represents relative distance between species in each body region in avian perceptual colour space. The unit of □????*S* is jnd (just noticeable difference), a value of 1 being the threshold value for discrimination of colours by birds.

Species comparison	Body region, □????*S*						
	Crown	Nape	Back	Rump	Throat	Chest	Belly
S. hypoxantha vs. *S. ruficollis*	8.53	6.42	6.82	5.47	5.37	6.00	4.06
S. hypoxantha vs. *S. hypochroma*	15.87	11.06	12.97	13.38	13.64	9.30	6.88
S. hypoxantha vs. *S. cinnamomea*	11.87	8.93	10.64	9.06	11.19	7.81	7.87
S. hypochroma vs. *S. ruficollis*	7.88	5.28	6.87	8.57	8.56	3.55	2.97
S. hypochroma vs. *S. cinnamomea*	4.37	2.30	2.39	4.68	2.48	1.53	1.88
S. cinnamomea vs. *S. ruficollis*	3.56	2.99	4.52	3.93	6.08	2.35	3.83

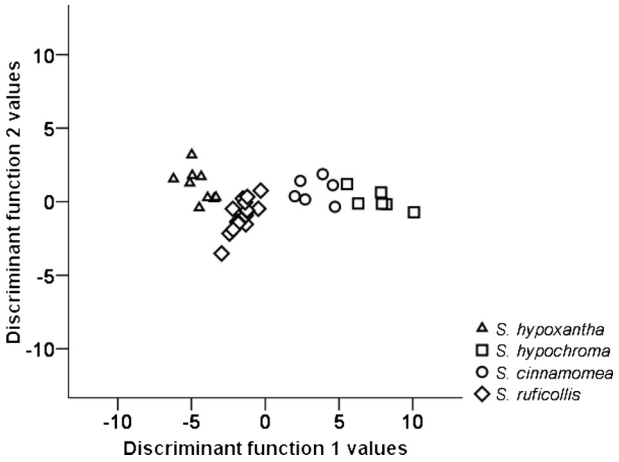

Figure 1. Distribution of individuals along the two discriminant function axes. The values for each individual in the space delimited by functions 1 and 2 are shown.

second discriminant function there is no separation among species. Jackknifed classification resulted in 97% of the cases correctly classified. *S. hypoxantha*, *S. cinnamomea* and *S. ruficollis* were always correctly classified, while 83.3% of the females of *S. hypochroma* were correctly classified (the misclassified specimen was placed as *S. cinnamomea*).

The loading matrix of correlations between predictors and discriminant functions shows that Q1 from crown and back, Q2 from crown, and Q4 from belly have the highest correlation with the discriminant functions (Table 2), considering a value of 0.3 a high correlation between a predictor and a function (Tabachnick and Fidell 2001). Because Function 1 accounts for the greatest variability between groups (95%) and shows a clear separation between species (Fig. 1), and Q1 from crown and back are the predictors with higher correlation with this function, these are the quantum catches that contribute the most to the separation among the four species. *S. hypoxantha* and *S. ruficollis* have a lower value of Q1 in both crown and back (crown mean = 38.70 ± 19.8 and 97.18 ± 12.2, back mean = 58.66 ± 20.7 and 109.61 ± 21.6, respectively) than *S. hypochroma* and *S. cinnamomea* (crown mean = 199.71 ± 69.3 and 132.91 ± 24.6, back mean = 219.7 ± 61.48 and 165.49 ± 21.1, respectively). In all four species, values of Q1 for the back are higher than values of Q1 for crown. When testing for the possibility of bias caused by skin age, no significant association was found between the two quantum catches with higher correlation with function 1 in the DFA (Q1 from crown and back) and the year of capture of the specimens (linear regression for Q1 from crown and back, $F = 1{,}41$ $p = 0.23$ and $F = 1{,}64$ $p = 0.21$, respectively).

Table 2. Matrix of loadings for the five predictor variables and their correlation with each of the discriminant functions. Values higher than 0.3 are considered a high correlation (Tabacknick and Fidell 2001).

Predictor	Correlation of predictor variables with discriminant function	
Variable	1	2
Q1crown	0.39	−0.39
Q2crown	0.19	−0.46
Q1back	0.42	−0.23
Q2back	0.16	−0.09
Q4belly	0.12	0.72

Discussion

This study reports previously unknown morphological divergence among females of four species of capuchinos, *S. hypoxantha*, *S. ruficollis*, *S. hypochroma*, and *S. cinnamomea*. Interspecific plumage colour distances between these species in avian visual space largely exceeded the threshold for colour discrimination in every plumage region measured and, thus, are predicted to be visually discernable by the birds (Table 1). Moreover, in 40 of the 42 comparisons (95.2%), distances were larger than twice the value of threshold ($\square????S > 2.0$ jnd), which suggests that colour differences should be distinguishable to birds even under non-ideal viewing conditions (Siddiqi et al. 2004). The largest differences found were between *S. hypoxantha* and the other three species, suggesting that females of this species have the most distinct plumage colouration. Because most specimens used in the study were collected in the same region (the Paraná-Paraguay Rivers basin, which is part of the area of sympatry of these species) we conclude that the differences found among species represent interspecific variation and are not the result of a sampling bias reflecting geographic variation in the species of the group.

The DFA model identified UV-wavelengths as particularly important in species separation. Since several studies have found UV wavelengths to have a significant role in sexual signaling (Bennett et al. 1996, 1997) and in species recognition (Bleiweiss 2004), the interspecific variation found suggests that potential UV plumage signals warrant particular attention in future colour studies of this group. Furthermore, aviary experiments of mate choice and species recognition using UV plumage colour manipulation would help to clarify the biological importance of the interspecific UV-wavelength variation found among these species of capuchinos.

A theoretical explanation for female ornaments, such as plumage colouration, has been that they are byproducts of ornamentation in males, which are shaped by sexual selection (Darwin 1871, Lande 1980). Therefore, the divergence in colouration among females of the capuchino species could simply be a byproduct of the divergence in male colouration. Comparison of male plumage divergence with female plumage divergence among these species showed several positive correlations for several plumage regions (unpublished data; available upon request). Additionally, this male-female correlation may not be the only factor driving female plumage colour evolution, and the interspecific variation found could be a compromise between a genetically correlated response and various selection pressures, such as habitat characteristics, sexual selection in females, or selection for species recognition. These four capuchino species are similar in their general habitat requirements (Stotz et al. 1996), but microhabitats, in terms of ambient light characteristics, have been shown

to be important aspects in signaling behavior, and resulting plumage divergence (e.g., Uy and Stein 2007). Currently lacking, are detailed studies of the light habitats used by these species. Also lacking, are data on active male choice of particular mates in these species, and male choice clearly needs to be tested explicitly, now, to address an hypothesis of sexual selection driving evolution of female characteristics, namely the plumage colour differences shown herein. Selection of traits to function as species recognition signals might be predicted among closely related sympatric species (McNaught and Owens 2002), where hybridization is likely (Tubaro and Lijtmaer 2002, Lijtmaer et al. 2003, Price 2003). This is indeed the case of the capuchinos, which had a recent and explosive radiation (Lijtmaer et al. 2004), and where hybridization has been recorded in the genus (Ouellet 1992). If hybrid offspring have a fitness disadvantage, the interspecific differences in female colouration found in this study could be selected for as species-specific signals that reinforce prezygotic isolation (Dale 2006). Cleary, behavioral data confirming the visual discrimination of these plumage colour differences, and detailed fitness information across hybrid zones are warranted.

To summarize, our analysis provides evidence of previously unknown female plumage colour evolution among capuchino species, and it is the first study to show cryptic female interspecific colour variation using an avian visual model. These colour differences are explained, at least in part, by the presence of a correlation between males and females in plumage divergence. Whether, and which, selection pressures might have played a role in the evolution of these differences are future questions that stem directly from our results. Use of an objective measure of plumage colouration in combination with the Vorobyev-Osorio model allowed us to identify ecological, behavioral, and evolutionary hypotheses that would not be possible to consider without quantification of these previously unknown differences in plumage colourartion among the four species of capuchinos. Furthermore, our study reinforces the notion that the human visual system can be misleading when assessing plumage colour in birds, and studies that fail to take this into account might miss potentially important biological information (Bennett et al. 1994, Eaton 2005, Eaton 2007).

Unlinked Reference

Price and Bouvier, 2003

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