

STAGES OF PLUMAGE MATURATION OF THE TAWNY-BELLIED SEEDEATER: EVIDENCE OF DELAYED PLUMAGE MATURATION AND CRYPTIC DIFFERENTIATION BETWEEN JUVENILES AND FEMALES

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Abstract. In some sexually dichromatic passerines, juvenile males retain a plumage similar to that of adult females through their first year or longer (delayed plumage maturation). The Tawny-bellied Seedeater (*Sporophila hypoxantha*) is a sexually dichromatic species in which, to the human eye, the juveniles look like females. We analyzed the species' stages of plumage maturation by reflectance spectrometry and a visual model of color discrimination on captive individuals of known ages. We found that males retain a plumage different from that of adult males through their first breeding season. By the time males passed the age of 1 year, their color did not differ from that of adult males in any region of the body except the crown. Spectrophotometry also revealed differences between the plumage color of juvenile males and females, and the color-discrimination model implies that the birds should be able to detect these differences. Thus juvenile males of the Tawny-bellied Seedeater acquire adult plumage after their first breeding season but are already dichromatic during the first year. How this pattern of plumage development affects the species' reproductive or other social behavior deserves further study.

Key words: avian visual modeling, plumage color, plumage reflectance, *Sporophila hypoxantha*, Tawny-bellied Seedeater.

Estadios de Maduración del Plumaje en *Sporophila hypoxantha*: Evidencia de Maduración Tardía del Plumaje y Diferenciación Críptica entre Machos Jóvenes y Hembras

Resumen. En algunas especies de paseriformes que presentan dicromatismo sexual los machos jóvenes retienen un plumaje similar al de las hembras durante el primer año de vida o más (maduración tardía del plumaje). *Sporophila hypoxantha* es una especie sexualmente dicromática en la que los jóvenes tienen la misma apariencia para el ojo humano que las hembras. Analizamos los diferentes estadios de maduración del plumaje utilizando espectrofotometría de reflectancia y un modelo visual de discriminación del color en individuos cautivos de edad conocida. Encontramos que los machos presentan maduración tardía del plumaje y retienen un plumaje diferente al del adulto durante la primera estación reproductiva. Cuando los machos alcanzaron más de un año de edad, su coloración del plumaje no difirió de la de los machos adultos para todas las regiones del cuerpo, excepto la corona. Los análisis espectrofotométricos revelaron diferencias entre el plumaje de los machos jóvenes y el de las hembras. El modelo de discriminación del color reveló que las diferencias espectrofotométricas podrían ser detectadas por individuos coespecíficos. Nuestros resultados mostraron que los machos jóvenes de *S. hypoxantha* adquieren el plumaje adulto después de la primera temporada reproductiva pero son sexualmente dicromáticos desde el primer año. Para determinar cómo este patrón de coloración del plumaje afecta los comportamientos sociales o reproductivos en esta especie son necesarios futuros estudios.

INTRODUCTION

For many years, studies of avian coloration have focused on colors resulting from the 400- to 700-nm portion of the light spectrum visible to humans (Bleiweiss 1997, Bowmaker et al. 1997). However, the acuity of human and avian visual systems diverge substantially (Bennett et al. 1997). Differences in visual capabilities between humans and birds and differences in the sensitivity of birds' photoreceptors have been found in

studies involving plumage color (Bennett et al. 1994, Bleiweiss 1997, Cuthill et al. 1999), and as a result many cases of sexual dichromatism cryptic to humans have been detected (Mahler and Kempnaers 2002, Eaton and Layon 2003, Eaton 2007, Bridge et al. 2008, Armenta et al. 2008). In particular, Eaton (2005) found that the majority of passerine species considered sexually monochromatic on the basis of human visual perception are actually sexually dichromatic from an avian

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perspective. These differences are not restricted to the region of the spectrum invisible to the human eye (300–400 nm) but also extend to the visible region (400–700 nm).

In most sexually dichromatic passerines, juveniles molt the entire body plumage before attempting their first breeding (first prebasic molt). In some species, however, males retain a plumage similar to that of females throughout the first year or longer (delayed plumage maturation, Lyon and Montgomerie 1986). The degree of delayed plumage maturation varies by species, with subadult males looking completely different from adult males in some species such as the North Island Robin (*Petroica longipes*; Powlesland 2002) but differing only subtly in others such as the Florida Scrub Jay (*Aphelocoma coerulescens*; Siefferman et al. 2008). Proposed explanations for delayed plumage maturation include adaptations to the breeding season or differences between the age classes' abilities to signal competitively (Rohwer et al. 1980, Lyon and Montgomerie 1986, Andersson 1994, Senar 2006, Siefferman et al. 2008).

The genus *Sporophila* (Emberizidae) comprises 31 species of small finches that inhabit grassy open and semi-open habitats from Mexico to central Argentina (Meyer de Schauensee 1952, Ridgely and Tudor 1989). Within this genus is a monophyletic group of 11 species (Lijtmaer et al. 2004), the capuchinos, with marked sexual dichromatism characterized by strongly patterned and colorful males and dull females in which the species are similar (Ridgely and Tudor 1989), although Benites et al. (2010) showed that females of some of these species (*S. hypoxantha*, *S. hypochroma*, *S. cinnamomea* and *S. ruficollis*) have differences in plumage coloration that should be detectable by birds.

The Tawny-bellied Seedeater (*Sporophila hypoxantha*) occurs in Bolivia, Brazil, Paraguay, Uruguay, and Argentina, where it is relatively common in areas with tall grass, especially near water. During the nonbreeding season it is usually associated with conspecifics and also with other species of seedeaters, with which it forms mixed flocks (Di Giacomo 2005). This species is sexually monomorphic in size, but like most others of the genus it has marked sexual dichromatism (Ridgely and Tudor 1989). Males are mostly brownish above, and have the rump and underparts tawny rufous, this color extending up to cover the cheeks and ear coverts, while females are brown above and buffy brownish below (Ridgely and Tudor 1989). The crown of the male is clear gray, that of the female brownish (Ridgely and Tudor 1989). Juvenile males are paler than adult males, and it is impossible for the human eye to distinguish them from females. Whether juvenile males molt into adult plumage before their first breeding or retain this female-like plumage through their first year and molt into adult plumage after their first breeding season has not previously been documented.

Among passerines, delayed plumage maturation is more frequent in species that forage in flocks than in those that forage solitarily (Beauchamp 2003). It is also more frequent in

dichromatic than in monochromatic species (Lyon and Montgomerie 1986, Beauchamp 2003) and in species in which females select mates on the basis of plumage coloration rather than on the basis of territory quality (Montgomerie and Lyon 1986). In agreement with this general pattern, Tawny-bellied Seedeaters forage in mixed flocks during the nonbreeding season (Di Giacomo 2005) and are sexually dichromatic.

We established a small captive population of Tawny-bellied Seedeaters and measured the plumage color of young birds at about 5–6, 12–13, and 16–17 months of age; we then compared these measurements to those of males and females that were 2 or more years of age. Using reflectance spectrometry and the Vorobyev–Osorio visual model of color discrimination (Vorobyev and Osorio 1998) to account for the sensitivity of avian photoreceptors, we analyzed plumage color for the entire wavelength range to which birds are sensitive.

METHODS

CAPTURE AND MAINTENANCE OF BIRDS

We mist-netted Tawny-bellied Seedeaters at Reserva El Bagual, Formosa Province, Argentina (26° 10' S, 58° 56' E), in early March 2007. From the end of March 2007 we kept them at the Faculty of Exact and Natural Sciences at the University of Buenos Aires. Birds were trapped under a permit from the Fauna Authority of Formosa Province and kept in captivity under a permit from the National Fauna Authority of Argentina. Immediately after bringing the birds to the facility we determined the sex of all individuals genetically (see below) and divided them into three groups: adult males (those in male adult plumage when captured, $n = 16$), juvenile males (those in juvenile/female plumage and with conspicuous gape flanges when captured and sexed as males, $n = 25$), and females ($n = 11$). One juvenile and three adult males died during the study. Birds were housed in wire cages of 120 × 40 × 40 cm in groups of 11–16 birds per cage (one cage with adult males, one with adult females, and two with juvenile males). Cages were arranged so that birds in different cages were visually but not acoustically isolated. The birds were maintained on a natural cycle of light and dark at room temperature, except during winter, when the minimum temperature was set to 15–18 °C (similar to the temperature in the species' winter range). Our study lasted 14 months, and during that period birds were provided with a diet of millet and canary seeds, vitamins, and water ad libitum.

SEX DETERMINATION

Following a standard protocol for the polymerase chain reaction and using primers P2 and P8 (Griffiths et al. 1998), we sexed the birds genetically by amplifying the highly conserved chromo-helicase-DNA-binding protein (CHD) gene located on the avian sex chromosome, which has introns that differ in length by sex (Ellegren 1996). We took a small blood sample (20–30 µL) by puncturing the brachial vein with a

31-gauge needle. Blood was collected with an 80- μ L heparinized capillary, immediately mixed with 0.5 mL of lysis buffer (100-mM Tris, pH 8, 10-mM NaCl, 100-mM EDTA, 2% SDS) and stored at room temperature until genetic analysis.

SEXUAL DIMORPHISM

We quantified plumage reflectance with an Ocean Optics S2000 spectrometer with a PX-2 pulsed xenon light source and a bifurcated fiberoptic probe (Ocean Optics, Inc.). Following Osorio and Ham (2002), we calibrated measures of reflectance against a white standard of barium sulfate and against a black standard (in this case with the light source off). The probe was housed in a black plastic tube to minimize incident ambient light. We kept the distance between the probe and the body surface constant (17.05 ± 0.1 mm); the angle of incidence of illumination and reflected light measured was 90° to the feather surface.

We took reflectance measurements from adult males, females, and young males at three times (Fig. 1): (1) July 2007, when adult males and females (definitive basic plumage, sensu Humphrey and Parkes 1959) were 18 months of age or older and young males were approximately 5–6 months of age (first basic plumage), (2) February 2008, when adult males and females (definitive alternate plumage) were 7 months older than when first measured and young males were approximately 12–13 months of age (first alternate plumage), and (3) June 2008, when adult males and females (definitive basic plumage) were 11 months older than when first measured and young males were approximately 16–17 months of age (second alternate plumage). In Figure 1 under Results we refer to the various measurements with the age of the young males. We measured four regions of the body, the throat, breast, belly, and crown, choosing these because they are homogeneously colored and their size allowed us to take more than one reflectance

measure. For each body region we took an average of three scans at arbitrary locations on the feathers. We took each measurement within a diameter of 6 mm and recorded reflectance from 350 to 700 nm in 0.35-nm steps (wavelengths between 300 and 350 nm showed considerable noise, and the values of reflectance were very low, so we did not include them in the analysis). We recorded data via the spectral-acquisition software package OOIBASE32 (Ocean Optics, Inc.). We took dark and white reference measurements immediately before measuring each individual in order to minimize any error associated with drift of the light source and sensor. For computing facilities and to eliminate artifactual “spikes” spectra were reduced to 138 values by taking median reflectance values every 3 nm. We chose the median because it is usually less sensitive to outliers than the mean (Cuthill et al. 1999).

We analyzed reflectance spectra by estimating the brightness, calculated as the sum of the reflectance (R) over the complete wavelength range ($\sum R_{350-700}$) and UV-blue, green and red chromas, calculated as the ratio between each region’s reflectance and total reflectance (UV-blue chroma = $\sum R_{350-499} / \sum R_{350-700}$, green chroma = $\sum R_{500-599} / \sum R_{350-700}$, and red chroma = $\sum R_{600-700} / \sum R_{350-700}$).

We recorded morphometric data on body mass and wing length of adult males, females, and juvenile males in May 2007 (young males approximately 3–4 months old) and June 2008 (young males approximately 16–17 months old). Body mass was recorded to the nearest 0.1 g with a spring scale, wing length to the nearest 1 mm with a wing ruler.

VISUAL MODEL OF COLOR DISCRIMINATION

We calculated discriminability of color (ΔS) between the various groups with the Vorobyev–Osorio color-discrimination model (Vorobyev and Osorio 1998) implemented with the package SPEC (Hadfield 2010). This model calculates a

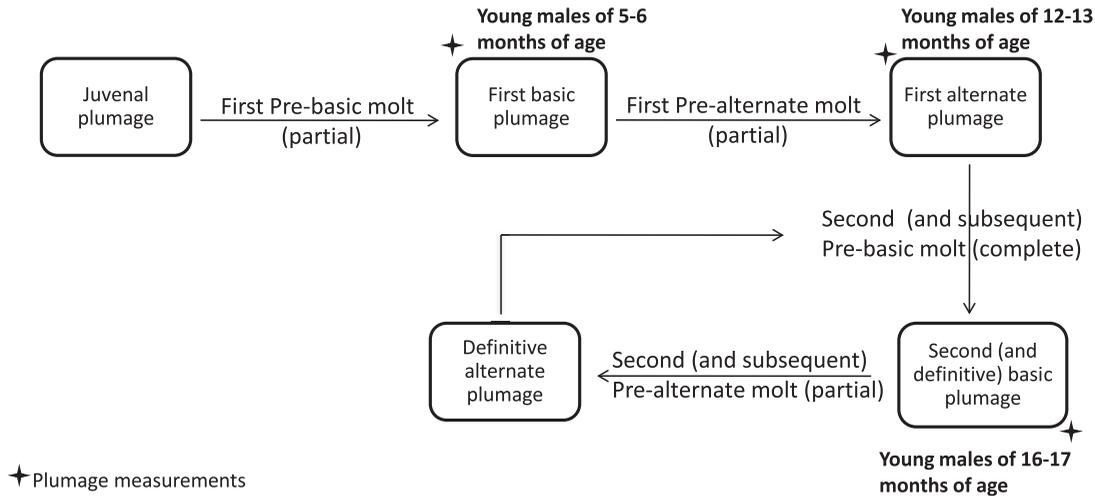


FIGURE 1. Molt and plumage succession of the Tawny-bellied Seedeater, *Sporophila hypoxantha* (adapted from Humphrey and Parkes 1959). Juvenal, first basic, and first alternate plumages correspond to young males, while adults alternate between definitive basic and alternate plumages. The prealternate molt precedes the reproductive season; the prebasic molt follows it.

distance in avian color space (ΔS) between two colors, defined by the quantum catches of each of the cone pigments in the avian retina (Eaton 2005). Values of ΔS are presented in units of “just noticeable differences” (jnd); ΔS values that exceed 1.0 jnd indicate a difference that can be detected by an avian visual system. The model incorporates the fact that the retinal cones do not use all the wavelengths equally and are more sensitive to some wavelengths than to others.

There are two major systems of bird vision, which are based mainly on the maximum sensitivity (λ_{\max}) of the UV/violet cones (see Hart et al. 2000, Hart 2001, Hart and Hunt 2007): violet sensitive (VS, $\lambda_{\max} = 403\text{--}426$ nm) and ultraviolet sensitive (UVS, $\lambda_{\max} = 355\text{--}380$ nm). The UVS system is found principally in the orders Passeriformes and Psittaciformes. Because of the complexity of the method used to examine the chromatic ocular disposition (e.g., Hart 2001), there is information for only a few species (see Hart 2001). Although closely related species tend to have similar values of λ_{\max} , avian phylogeny is not the only explanation for the distribution of the UVS/VS systems; there is also an adaptive explanation (Hart 2001, Odeen and Hastad 2003). Since the chromatic ocular disposition of the Tawny-bellied Seedeater or any species of *Sporophila* has not been measured, we used data for the Blue Tit (*Cyanistes caeruleus*; Hart 2001). We based our decision on two reasons: (1) the passerines that have been studied have the UVS visual system, except for the corvids, which have the VS system. Moreover, the maximum sensitivity varies little by species (see Hart et al 2000, Odeen and Hastad 2003), and (2) the Blue Tit’s visual system has been used in the study of more than 100 species of Passeriformes (Eaton 2005) and four species of *Sporophila* (Benites et al. 2010). In particular, Benites et al. (2010) recalculated the color-space distance by using proportions of cone-cell types of *Turdus merula* and *Sturnus vulgaris*, two species that encompass the known variation among passerines (Hart 2001), and the results did not alter any conclusions.

STATISTICAL ANALYSIS

We used Pearson correlations to examine associations among body regions and different spectral variables. We analyzed spectral variables with repeated-measures ANOVA and post-hoc Tukey tests, differences in body size with ANOVA and discriminant analysis. For statistical analyses, we used Statistica version 8.0 (StatSoft). All P -values are two-tailed with α set at 0.05. Data are presented as means \pm SE.

RESULTS

SEXUAL DICHROMATISM AND PLUMAGE MATURATION

Values of reflectance of the throat, breast, and belly were highly correlated ($r = 0.57$ to 0.91 , $P < 0.05$ for the three comparisons between these three areas), so we present the results of breast and crown reflectance only.

Tawny-bellied Seedeaters have two molts per year, the prealternate and prebasic, which precede and follow the reproductive season, respectively. The first two molts and second (and subsequent) prealternate molt are partial, encompassing the throat, breast, crown, back, and rump, whereas the second (and subsequent) prebasic molts are complete. After juvenal plumage, males have three different plumages (first basic, first alternate, and second basic) before acquiring the definitive alternate and basic plumages (Fig. 1). Adults alternate between definitive basic and alternate plumages during the cycle.

Figure 2 shows reflectance spectra of the breast and crown of adult males, females, and young males at the three stages of maturation we measured. Reflectance of the breast was greatest in the red (600–700 nm), of the crown in the UV-blue (350–500 nm) (Fig. 2). Because the different chromas are not independent, we used only those that best represent breast and crown reflectance (red and UV-blue chroma, respectively).

We performed repeated-measures ANOVAs with groups (adult male, female, or young male) as a between-subject factor, time (first, second, or third measurement) as a within-subject factor, and breast brightness, red chroma of the breast, crown brightness, and UV-blue chroma of the crown as dependent variables. For breast-color variables, we found significant differences between groups (brightness: $F_{2,43} = 50.2$, $P < 0.0001$; red chroma: $F_{2,43} = 45.17$, $P < 0.0001$) and time (brightness: $F_{2,86} = 8.2$, $P < 0.01$; red chroma: $F_{2,86} = 10.08$, $P < 0.0001$) and a significant interaction between groups and time (brightness: $F_{4,86} = 7.6$, $P < 0.01$; red chroma: $F_{4,86} = 19.72$, $P < 0.0001$). For crown coloration, we found significant differences between groups (brightness: $F_{2,42} = 20.2$, $P < 0.0001$; UV-blue chroma: $F_{2,42} = 19.73$, $P < 0.0001$) and time (brightness: $F_{2,84} = 471.1$; $P < 0.0001$, UV-blue chroma: $F_{2,84} = 126.06$, $P < 0.0001$) and a significant interaction between groups and time (brightness: $F_{4,84} = 41.8$, $P < 0.0001$; UV-blue chroma: $F_{4,84} = 8.13$, $P < 0.0001$). The breast brightness of young males but not that of adult males and females changed over time, while the red chroma of both groups of males changed over time. For crown coloration we found differences over time in brightness of adult and young males and in UV-blue chroma for all groups.

The breast plumage of adult males had values of brightness lower and red chroma greater than those of females in the three measurements ($P < 0.001$ for all comparisons; Figs. 3 A, B). The breast plumage of males 5–6 months old (juveniles) and 12–13 months old had values of brightness greater and red chroma lower than those of adult males ($P < 0.001$), but by the age of 16–17 months these values became undistinguishable from those of adult males ($P > 0.05$, Figs. 3 A, B). Values for the breasts of males of 5–6, 12–13, and 16–17 months of age also differed from that of females (Figs. 3 A, B), being lower in brightness than that of females ($P < 0.001$). When males were 16–17 months of age their values for red chroma were greater than that of females ($P < 0.0001$, Figs. 3 A, B).

The crowns of adult males had values of brightness and UV-blue chroma greater than those of females in all three measurements ($P < 0.001$ for all comparisons, Fig. 3 C, D). The crowns of males 5–6 months old had a value of brightness lower than that of females ($P < 0.05$) and values of brightness and UV-blue chroma lower than those of adult males ($P < 0.001$, Figs. 3 C, D). The crowns of males 12–13 and 16–17 months old had values of brightness and UV-blue chroma greater than those of females ($P < 0.001$ and $P < 0.01$,

respectively, Figs. 3 C, D). Finally, the crowns of males of 16–17 months old had values of UV-blue chroma lower than that of adults ($P < 0.001$, Figs. 3 C, D).

The color-discrimination model showed that the breast and crown colors of adult males differed from those of females in the three measurements (breast: $\Delta S > 1.11$ jnd and crown: $\Delta S > 2.01$ jnd), while the breast colors of young and adult males differed in the first and second measurements ($\Delta S = 1.37$ jnd and $\Delta S = 1.22$ jnd, respectively) but became indistinguishable

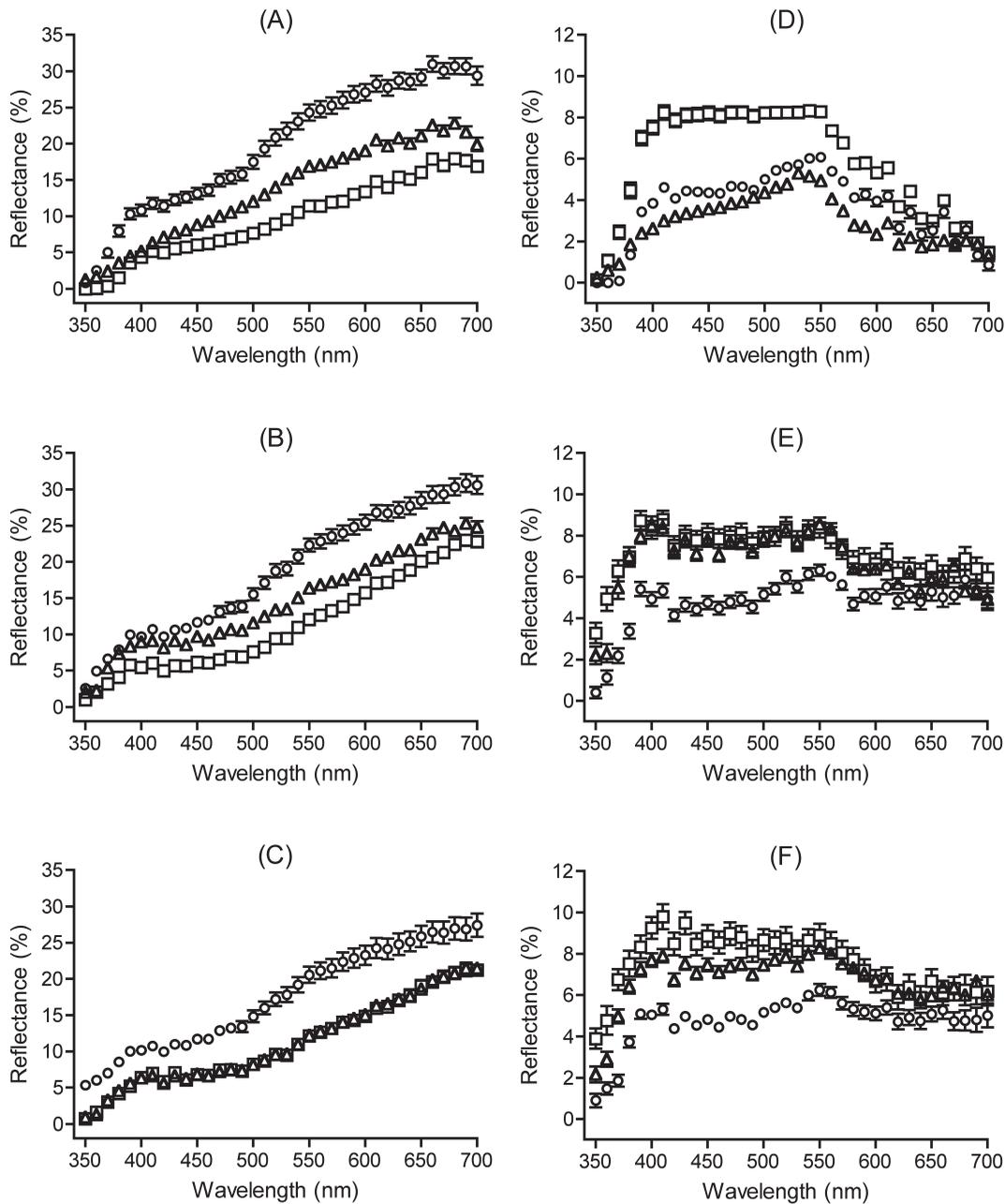


FIGURE 2. Reflectance spectra (mean \pm SE) of the breast (left column) and crown (right column) of adult males (squares), females (circles), and young males (triangles) of the Tawny-bellied Seedeater, *Sporophila hypoxantha*, when young males were 5–6 months old (A and D), 12–13 months old (B and E), and 16–17 (C and F) months old.

in the last one ($\Delta S = 0.56$ jnd). Young and adult males also differed in all measurements for crown coloration ($\Delta S > 1.22$ jnd). Finally, young males and females differed in all measurements for breast ($\Delta S > 1.11$ jnd) and crown coloration ($\Delta S > 1.13$ jnd).

In summary, in males, the first basic, first alternate, and second basic plumages differed from the definitive basic and alternate plumages, respectively. After the second prealternate molt, maturing young males acquired the definitive alternate plumage and did not differ from older males (Facchinetti, unpubl. data). Also, males' plumage differed from females' plumage in all stages of plumage maturation.

SIZE DIMORPHISM

Wing length differed by group when we took the first measurement, when juvenile males were 3–4 months of age ($F_{2,48} = 3.12, P = 0.05$). Adult males had wings longer than females' (51.5 ± 5 vs. 49.8 ± 5 mm, post hoc test $P < 0.05$), but there were no differences between juvenile and adult males (50.9 ± 3 mm, post hoc test $P > 0.05$) or between juvenile males and females (post hoc test $P > 0.05$). We did not detect differences in body mass between adult males (10.01 ± 0.21 g, $n = 16$), females (10.17 ± 0.25 g, $n = 11$), and juvenile males of 3–4 months of age (10.17 ± 0.16 g, $n = 25; F_{2,48} = 0.21, P = 0.81$). At the second measurement (age 16–17 months), the

wing length of maturing males did not differ from that of adult males (51.9 ± 3 vs. 51.6 ± 4 mm), but both had wings longer than those of females (49.8 ± 4 mm, $F_{2,44} = 7.85, P < 0.001$ and contrasts $P < 0.02$). Also, a discriminant analysis using the three morphological variables did not detect differences between males (Wilks' $\Lambda = 0.86, F_{3,32} = 1.6, P = 0.19$).

DISCUSSION

The Tawny-bellied Seedeater molts twice per year (prealternate and prebasic molts), before and after the breeding season. Immature birds are distinguishable from adult males and females during their first two years. Only at the second prealternate molt do males acquire their definitive alternate plumage, after which they switch between definitive alternate and basic plumages each cycle (Fig. 1). Before acquiring the definitive plumage, males molt into three consecutive different plumages (first basic, first alternate, and second basic). The first alternate and basic plumages correspond to first-year individuals, the second basic plumage corresponds to second-year individuals, and all differ from males' definitive alternate and basic plumages (two years or more).

As expected, adult males had brighter crowns and darker breasts than females as well as differences in measurements

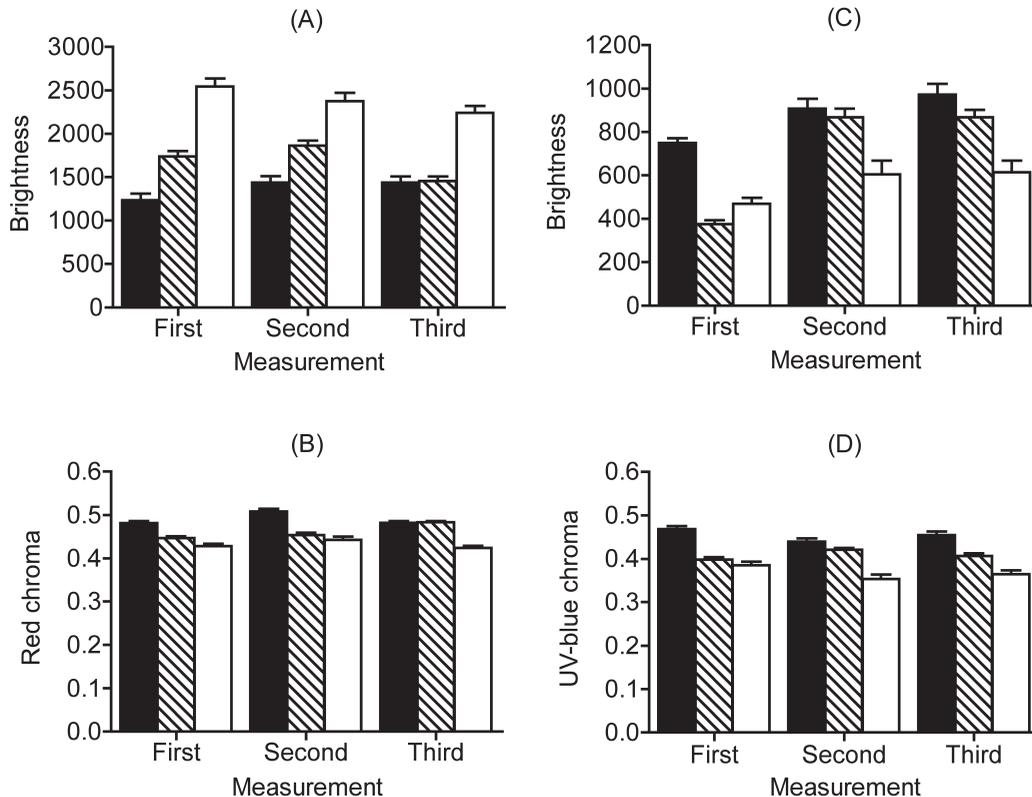


FIGURE 3. Brightness of breast (A), red chroma of breast (B), brightness of crown (C), and UV-blue chroma of crown (D) of adult males (black), females (white) and young males (striped) of the Tawny-bellied Seedeater, *Sporophila hypoxantha*, for the three measurements (when young males were 5–6 months, 12–13 months, and 16–17 months of age). Height of bar indicates mean (\pm SE).

and the shape of the spectrum shape in all body regions. Less expected were the clear differences between females and juvenile males, given that these two groups cannot be distinguished by human vision. These differences were present not only in the UV region of the spectrum but also in the visible region. Moreover, using the visual model of color discrimination of Vorobyev and Osorio (1998), we found that the differences in plumage coloration detected by the spectrophotometer were also probably detectable by the birds. This indicates that Tawny-bellied Seedeaters have the capacity to perceive differences in plumage coloration between females and juvenile males. Our results add to previous evidence (Eaton 2005) by showing another example of intraspecific differences in plumage color in the UV and visible spectrum that are concealed to the human eye.

We found clear differences between the plumages of juvenile males and females and between males' first basic, first alternate and second basic plumages and males' definitive basic and alternate plumages. In addition, we found that juvenile males differ from adult males in breast and crown color until their second prealternate molt. Tawny-bellied Seedeaters do not acquire the definitive alternate plumage before their first attempt at breeding and still look different from adults during their first breeding season. Thus the male's plumage coloration is an age-dependent signal that could be used by females in mate choice. Also, plumage maturation is delayed until after the second prebasic molt, as males of 16–17 months of age differ from older males in crown color, until their second prealternate molt.

Hypotheses for the adaptiveness of delayed plumage maturation have focused on the benefits that juveniles may obtain by showing their youth and inexperience (status-signaling hypothesis, Lyon and Montgomerie 1986). The adaptive significance underlying delayed plumage maturation in the Tawny-bellied Seedeater is currently unclear, but, in light of the species' biology and previous studies, the delay could act as a signal to avoid aggression from older males, during either the reproductive or the nonreproductive season. Furthermore, it may be an adaptation that shows juveniles' inexperience to females during mate choice. However, it is still unknown whether females of this species select mates on the basis of plumage coloration and if one-year-old males establish territories. Since most species of *Sporophila* are markedly dichromatic sexually (Ridgely and Tudor 1989) and juvenile males are apparently undistinguishable from females, it would be interesting to study whether the pattern we observed in the Tawny-bellied Seedeater occurs in other species of the genus.

The pigment responsible for the Tawny-bellied Seedeater's brown coloration is melanin (transmission electron microscopy, B. Mahler unpubl. data). On the other hand, the male's crown coloration seems to be structurally based, as its spectral curve resembles curves of other species with structural coloration, such as those of the dorsal feathers of the Barn Swallow (*Hirundo rustica*) (Perrier et al. 2002), or the

blue of the male Western Bluebird (*Sialia mexicana*) (Budden and Dickinson 2009). Studies of the function of pigment and structurally based coloration have shown that plumage coloration may act as a signal of a male's competitive ability and social dominance (Senar 1999, Quesada and Senar 2007), quality (Keyser and Hill 2000), or parental quality (Roulin et al. 2001, Siefferman and Hill 2003, 2005), and it may be involved in mate choice (Kigma et al. 2008).

To summarize, our study demonstrates delayed plumage maturation and discloses differences in plumage color between Tawny-bellied Seedeaters of different age classes that were previously unknown. Females and juvenile males, which to the human eye appear not to differ, do differ in plumage color, and these differences should be detectable by the birds. Furthermore, young and adult males differ in crown coloration after the second prebasic molt. These results support the importance of using models of avian vision in plumage studies and suggest a role of plumage differences in avian communication, not only between the sexes but between individuals of different ages.

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