

BLUE MALES AND GREEN FEMALES: SEXUAL DICHROMATISM IN THE BLUE DACNIS (*DACNIS CAYANA*) AND THE SWALLOW TANAGER (*TERSINA VIRIDIS*)

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Resumen. – Machos azules y hembras verdes: dicromatismo sexual en el Saí Azul (*Dacnis cayana*) y la Tersina (*Tersina viridis*). – Las diferencias entre sexos en la coloración del plumaje, conocidas como dicromatismo sexual, son un fenómeno común entre los fruteros Neotropicales (familia: Thraupidae). En muchas especies de este grupo, el dicromatismo sexual es percibido, por observadores humanos bajo condiciones de luz natural, como machos azules y hembras verdes. Por ejemplo, este patrón es recurrente en especies de varios géneros, tales como *Chlorochrysa*, *Tangara*, *Dacnis*, *Chlorophanes*, *Cyanerpes* y *Tersina*. Con el objetivo de entender la naturaleza física de este fenómeno, y de determinar el grado de similitud y/o diferencia en el dicromatismo sexual exhibido por diferentes especies, describimos la coloración del plumaje del Saí Azul (*Dacnis cayana*) y la Tersina (*Tersina viridis*) mediante espectrofotometría de reflectancia. No se encontraron diferencias sexuales en el tono de ambas especies. En cambio, los machos mostraron un pico de reflectancia secundario en la región de longitudes de onda corta (UV a violeta), el cual estuvo ausente en las hembras. Este patrón de reflectancia bimodal de los machos difiere de los patrones unimodales más comúnmente descritos en plumajes azules. Dada la similitud en los espectros a través de los cuales ambas especies estudiadas adquieren el mismo dicromatismo sexual azul-verde, sumado a que la evidencia molecular indica una relación cercana entre los géneros *Tersina* y *Dacnis*, interpretamos el marcado dicromatismo sexual encontrado en el Saí Azul y la Tersina como una condición homóloga.

Abstract. – Sexual differences in plumage coloration, referred to as sexual dichromatism, are a common phenomenon among tanagers (family Thraupidae). In many species of this group, sexual dichromatism is perceived, by human observers under natural light conditions, as blue males and green females. For instance, this pattern is recurrent among species of several genera, such as *Chlorochrysa*, *Tangara*, *Dacnis*, *Chlorophanes*, *Cyanerpes* and *Tersina*. To understand the physical nature of this phenomenon, and to assess the degree of similarity/difference in sexual dichromatism exhibited by different species, we described the plumage color of the Swallow Tanager (*Tersina viridis*) and the Blue Dacnis (*Dacnis cayana*) using reflectance spectrophotometry. In both species there were no sexual differences in hue. Instead, males showed a secondary peak of reflectance in the short-wavelength (UV-violet) part of the spectrum, which was absent in females. This bimodal reflectance shape of males is different from the most commonly found unimodal pattern of blue plumages. Given the spectral similarity by which both studied species achieve the same blue-green sexual dichromatism, and the fact that molecular evidence indicates a close relationship between the genera *Tersina* and *Dacnis*, we interpret the particular sexual dichromatism found in both the Swallow Tanager and the Blue Dacnis as a homologous condition. *Accepted 3 June 2008.*

Key words: Plumage evolution, reflectance spectrophotometry, sexual dimorphism, Thraupidae, *Tersina viridis*, *Dacnis cayana*.

INTRODUCTION

Sexual differences in plumage coloration, hereafter referred to as sexual dichromatism, are a very common phenomenon among tanagers (family Thraupidae). About half of the more than 240 species of this group shows a strongly marked sexual dichromatism (Burns 1998, Isler & Isler 1999), and probably many more show cryptic (i.e., undetectable by humans without the assistance of a spectrophotometer) sexual dichromatism (Eaton 2005, Tubaro *et al.* 2005). Among the species that are sexually dichromatic, there is a recurrent pattern of variation of blue males and green females, present in different genera such as *Tersina*, *Dacnis*, *Chlorophanes*, *Cyanerpes*, *Chlorochrysa* and *Tangara*. Ambient light has been proposed as a factor driving the color properties of the plumage of birds, since it could enhance or reduce its conspicuousness (McNaught & Owens 2002, Gomez & Théry 2004, Théry 2006). According to Théry (2006), blue and green patterns would be favored in species that inhabit the canopy. In this forest stratum, UV and blue wavelengths prevail in the ambient light, which would increase the brightness of short-wavelength reflecting plumages, while green colors would promote crypsis by matching plumage and background coloration (Endler 1993, Gomez & Théry 2004). However, the presence in the forest understory of many species with UV reflecting skin coloration (Prum & Torres, 2003) seems to contradict this hypothesis. Moreover, color correction in the avian visual system would be accurate enough to compensate the possible effects of the ambient light in color perception (Endler *et al.* 2005, Stoddard & Prum 2008). Therefore, the factors driving color patterns in bird's plumage remain speculative to date.

Short-wavelength colors, such as violet and blue, are a product of the coherent scattering and constructive interference of short wavelengths on the periodic microstructure of feather's barbs and barbules (Prum *et al.* 1998, Andersson 1999, Prum 1999, 2006; Shawkey *et al.* 2003, 2005). Medium wavelength colors, such as green, result from either the presence of pigments, feather microstructure, or both (Dyck 1971, Prum 1999, 2006). In general, short-wavelength colors also reflect light in the near UV part of the spectrum that is invisible to humans but visible to birds (Cuthill *et al.* 2000b, Eaton & Lanyon 2003). Birds also differ in other aspects of their visual system, including the presence of four types of single cones in their eye's retina instead of the three present in the human eye (Bennett & Cuthill 1994, Bowmaker *et al.* 1997). Thus, the use of human perceptual standards for describing plumage coloration and its evolutionary significance is, at best, inadequate (Cuthill *et al.* 2000a, 2000b). Recent studies have applied reflectance spectrophotometry to describe objectively the plumage color in tanagers, including differences between cryptic species (Bleiweiss 2004a), species guilds (Bleiweiss 2004b, 2005), and cryptic sexual dichromatism (Tubaro *et al.* 2005).

The Swallow Tanager (*Tersina viridis*) and the Blue Dacnis (*Dacnis cayana*) are two species of tanagers that inhabit mainly in the canopy of forests and are broadly distributed from Central America south to Argentina (Isler & Isler 1999). In both species the blue-green sexual dichromatism pattern is strikingly marked. Males exhibit bright blue plumage while females appear green to human observers under natural light conditions. Although these two species are easily distinguishable because their morphology is differ-

ent, they are closely related (Burns 1997, Burns *et al.* 2003) and they show a remarkable similar sexual dichromatism pattern, at least to the naked eye. It is the purpose of this study to describe the plumage's reflectance properties of both sexes in these two species and to compare them intra and inter-specifically, as an approach to the underlying mechanisms that produce this pattern, in an objective and quantitative way that is independent of human color perception and that can be more easily related to avian perceptual capabilities.

METHODS

This study was conducted on study skins deposited at the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia." Only specimens in perfect condition (without evidence of degradation due to poor storage conditions or defects in preparation), and with complete information on sex, locality, and date of collection were included. A total of 16 adult individuals of the Swallow Tanager (9 males and 7 females) and 12 adult specimens of the Blue Dacnis (6 males and 6 females) were included.

Reflectance spectrophotometry. Reflectance measurements were taken from four plumage patches: crown, rump (upper and lower), wing coverts (right and left, hereafter referred to as coverts) and chest (measured twice in the Swallow Tanager and once in the Blue Dacnis). These regions were chosen for two reasons: a) they appear homogeneously colored, and b) their size allowed us to take at least one reflectance measurement. For those plumage patches measured more than once, we used the mean for each individual in subsequent analysis.

Plumage reflectance was measured using an Ocean Optics 2000 spectrophotometer (Ocean Optics, Inc., Dunedin, Florida) with a

PX-2 pulsed xenon light source (effective range of emission from 220 to 750 nm) calibrated against a white standard of barium sulphate following Osorio & Ham (2002). Before the measurement of each individual, a new calibration was done to correct for possible shifts in the performance of the equipment. Plumage was illuminated and reflected light collected at 45° to the surface and from the proximal end of the feather. This procedure was adopted to avoid the effect of specular reflectance that could result when the feather is illuminated and reflected light is collected perpendicular to its surface (Andersson 1996). The probe was mounted in a prismatic probe holder, which isolates the measured surface from ambient light, and was held over the selected plumage patch of the study skin. The diameter of the circular region illuminated and measured was 6 mm, and the distance between the probe and the plumage was 23 mm. The spectrophotometer resolution was 0.35 nm. Each spectrum was the average of three readings with an integer time of 100 ms. Boxcar smoothing was not performed.

Statistical analysis. In order to reduce the amount of information and to smooth the shape of the spectra we calculated the median reflectance values for bins of 5 nm in the wavelength range from 320 to 700 nm. Four spectral variables, estimated from the spectra, were used to describe plumage coloration. Brightness was estimated as the sum of reflectance values over the entire spectrum ($\Sigma R_{320-700}$). Hue was calculated as the wavelength of maximum reflectance (λ_{Rmax}). Chroma was estimated as the reflectance 50 nm around the hue divided by total reflectance ($R_{(\lambda_{Rmax} \pm 50nm)} / R_{320-700}$). This range represents approximately the sensitivity range of the MWS (medium wavelength sensitive) cone of birds that extends for about 100 nm and which maximum coincides with the average hue we

TABLE 1. Sexual dichromatism in hue (λ_{Rmax} ; expressed in nm) of different plumage patches for the Swallow Tanager (*Tersina viridis*) and the Blue Dacnis (*Dacnis cayana*). Values are means \pm SD and Mann-Whitney *U*-test results.

Plumage patch	Swallow Tanager				Blue Dacnis			
	Males	Females	<i>U</i>	<i>P</i>	Males	Females	<i>U</i>	<i>P</i>
	(n = 9)	(n = 7)			(n = 6)	(n = 6)		
Crown	562.80 \pm 7.08	570.63 \pm 10.32	11.0	0.031	542.02 \pm 6.63	545.35 \pm 4.16	11.5	0.310
Rump	552.82 \pm 7.89	561.37 \pm 11.06	16.5	0.114	542.85 \pm 7.05	550.32 \pm 5.22	7.0	0.093
Chest	558.34 \pm 5.82	564.25 \pm 9.87	17.5	0.142	545.35 \pm 4.16	555.29 \pm 6.08	3.0	0.015
Coverts	555.56 \pm 5.61	563.52 \pm 12.02	19.5	0.210	541.19 \pm 4.08	550.32 \pm 8.75	7.5	0.093

$\alpha = 0.01$ after Bonferroni correction.

found (Table 1, Bowmaker *et al.* 1997). Because of the importance of UV in visual perception in birds, we also calculated a value of “UV chroma” as the relative reflectance of UV wavelengths from 320 to 400 nm to overall reflectance ($R_{320-400}/R_{320-700}$). Finally, if a secondary peak of reflectance was present in the UV-violet part of the spectrum we registered its wavelength ($\lambda_{\text{secondary peak}}$).

Even though the age of the specimens used for this study is very similar, i.e., they were collected less than 50 years apart, we evaluated possible effects of color fading due to museum storage on the study skins. We found no significant correlation between spectral variables and year of capture, in agreement with other studies (Mc Naught & Owens 2002, Bridge & Eaton 2005, Barreira *et al.* 2007, results not shown). Therefore, we did not control for fading effects due to museum storage in subsequent analyses.

Since the number of individuals in our samples was relatively small, and the homoscedasticity assumption of parametrical tests was not fulfilled in some cases, we used a non-parametrical test to evaluate color variation. We tested for sexual differences in each spectral variable and plumage patch using Mann-Whitney *U*-tests for the Swallow Tanager and the Blue Dacnis, separately. We also

compared coloration between species, for each sex separately, using this same statistical test. Finally, and given the fact that we used five different variables for describing the coloration of each plumage patch, we applied the Bonferroni correction to all comparisons, reducing the α level to 0.01 in order to keep the global type I error smaller than 5%.

RESULTS

Brightness was higher in males than in females in all plumage patches of the Swallow Tanager ($U = 0, P < 0.001$, Fig. 1). The crown and chest of the Blue Dacnis showed no significant sexual differences ($U = 6, P = 0.065$), while rump and coverts were brighter in males ($U = 2, P = 0.009$, Fig. 1). When compared between species, brightness was higher in males of the Swallow Tanager in crown and coverts ($U = 0, P = 0.001$), but showed no significant differences between males of both species in rump and chest after Bonferroni correction ($U = 8, P = 0.026$, Fig. 1). In contrast, female brightness of the Blue Dacnis was higher than that of Swallow Tanager, which is related to higher reflectance in the UV region of the spectra (Fig. 1), in all plumage patches ($U = 3, P = 0.008$) but coverts ($U = 11, P = 0.181$).

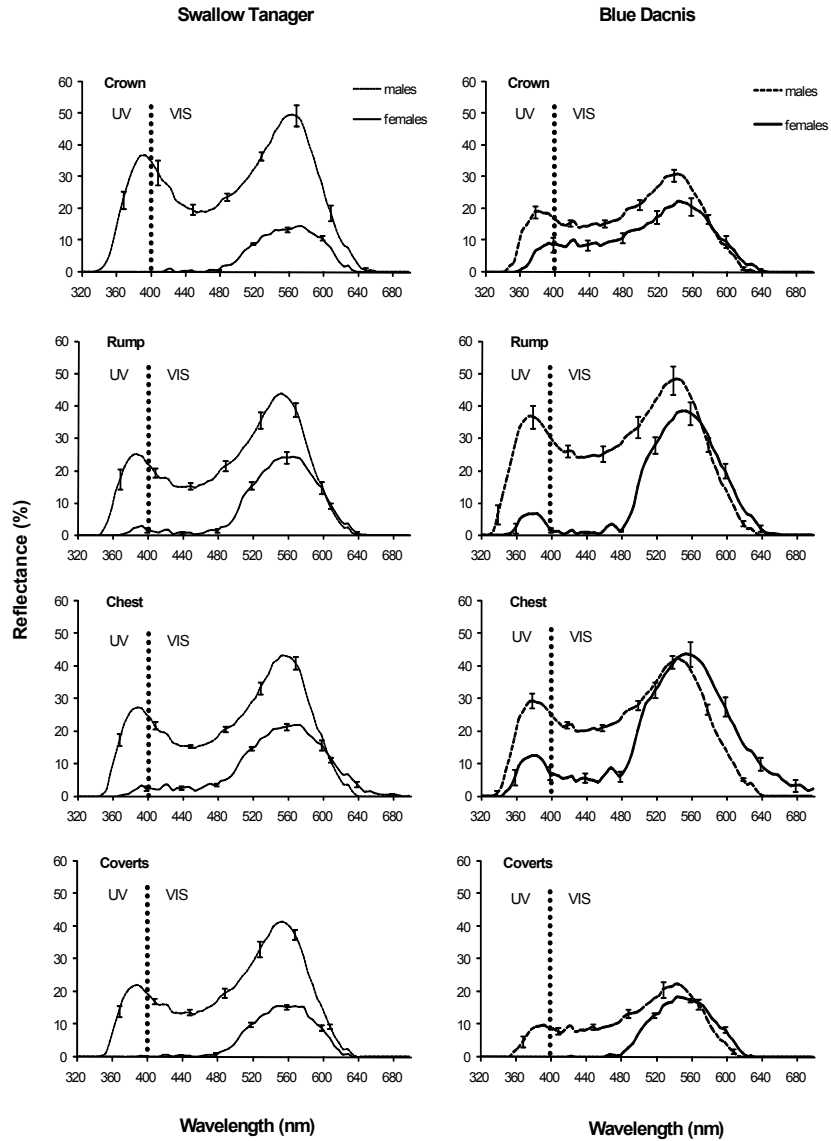


FIG. 1. Mean reflectance spectra (\pm SE) of the Swallow Tanager (*Tersina viridis*) and the Blue Dacnis (*Dacnis cayana*) of the four studied plumage patches according to sex.

In both species, males and females exhibited a high peak of reflectance at medium wavelengths (Fig. 1). Therefore, hue as defined was located approximately in the middle of the visible spectrum, corresponding to

green wavelengths in both sexes and species (Table 1). Although males had a slightly lower hue than females, this difference was only marginally significant after Bonferroni correction in the chest of the Blue Dacnis (Table 1).

TABLE 2. Interspecific differences in wavelength of maximum reflectance of the secondary peak ($\lambda_{\text{secondary peak}}$; expressed in nm) between males of the Swallow Tanager (*Tersina viridis*) and the Blue Dacnis (*Dacnis cayana*). Values are means \pm SD and Mann-Whitney U -test results.

Plumage patch	Swallow Tanager (n = 9)	Blue Dacnis (n = 6)	U	P
Crown	390.60 \pm 04.34	381.22 \pm 06.00	4.5	0.005*
Rump	386.20 \pm 06.52	377.02 \pm 07.42	8.5	0.026
Chest	389.50 \pm 03.45	379.53 \pm 06.79	5.0	0.008*
Coverts	386.22 \pm 04.28	407.06 \pm 28.56	19.0	0.388

*Significant after Bonferroni correction, $\alpha = 0.01$.

Nevertheless, males of the Swallow Tanager had significant higher hue than males of the Blue Dacnis in all patches ($U = 2$, $P = 0.002$) except for the rump ($U = 9$, $P = 0.036$, Table 1), while hue of females only differed significantly between species in the crown ($U = 1.5$, $P = 0.002$), being lower in the Blue Dacnis (Table 1). A strong secondary reflectance peak in the short-wavelength part of the spectrum, however, was only present in males of both species (Fig. 1). The wavelength of maximum reflectance of this secondary peak was located between 377 and 407 nm, corresponding to UV to violet colors, and showed significant interspecific differences in crown and chest, being slightly smaller in Blue Dacnis males (Table 2).

In both species, males always exhibited a higher UV chroma than females ($U = 0$, $P = 0.002$, Fig. 1) due to the presence of the secondary reflectance peak exclusively in this sex. When species were compared, only the rump UV chroma differed significantly between males, being higher for the Blue Dacnis ($U = 5$, $P = 0.008$), while UV chroma of females differed in the crown and chest, where it was higher for the females of the Blue Dacnis ($U = 2$, $P = 0.005$, Fig. 1).

In contrast to the results of UV chroma, males of both species had a lower chroma than females as a consequence of their higher total reflectance across the spectrum and the

presence of the secondary reflectance peak in the short-wavelengths ($U = 2$, $P = 0.009$, Fig. 1). Chroma also differed between species for the males in rump and chest ($U = 0$, $P = 0.001$) but in this case, it was higher for the Swallow Tanager. Females showed interspecific differences in chroma only in the crown ($U = 0$, $P = 0.001$) where it was higher also for the Swallow Tanager.

DISCUSSION

We have shown clear differences in the reflectance spectra between sexes in the Swallow Tanager and the Blue Dacnis. Surprisingly, while both sexes had the same hue, located in green wavelengths, only the males had a secondary reflectance peak in the short-wavelength (UV-violet) part of the spectrum. We also found significant sexual differences in brightness, chroma, and UV chroma, which are probably related to the presence of this secondary peak in the males' spectra. This particular feature produces the human perception that males are blue and females are green. This sexual dichromatism is probably stronger to birds themselves, because the secondary peak of reflectance extends into the near UV part of the spectrum that is visible to birds but not to humans. The bimodal reflectance spectra pattern described here for the males of these two species is uncommon

among blue plumages which generally appear with a single reflectance peak in the UV-blue range of wavelengths. This is the case of the blue plumages described, for instance, for the Blue Tit (*Parus caeruleus*, Anderson *et al.* 1998, Hunt *et al.* 1998), the Bluethroat (*Luscinia svecica svecica*, Johnsen *et al.* 1998), the Eastern Bluebird (*Sialia sialis*, Siefferman & Hill 2003), the Diademed Tanager (*Stephanophorus diadematus*, Tubaro *et al.* 2005), the Ultramarine Grosbeak (*Cyanocompsa brissonii*, Barreira *et al.* 2007, Stoddard & Prum 2008), and the Varied Bunting (*Passerina versicolor*, Stoddard & Prum 2008).

The mechanisms by which the plumage coloration of females and males of the two studied species are achieved remain unknown to date, and there are not proposed hypothesis to explain these phenomena. Only rarely does green plumage derive from the presence of green pigments (Dyck 1987, 1992), it seems reasonable to assume that the main peak of reflectance in the spectra of the Swallow Tanager and the Blue Dacnis females results from the nano-scale structure of the feather barbules alone or in combination with yellow pigments (Prum 2006, Shawkey & Hill 2005). A plausible explanation for the bimodal shape of the reflectance spectra of males is the presence of carotenoid pigments that absorb the short wavelengths of the visible spectrum but not the near UV ones, superimposed to a feather microstructure that reflects all wavelengths but the longer ones of the visible range. Carotenoid pigments are common in tanagers (Bleiweiss 2004b, 2005), but its presence in the Swallow Tanager and the Blue Dacnis has not been chemically confirmed yet. Moreover, the absence of this secondary peak of reflectance in females could be a consequence of a different feather microstructure or the presence of another pigment that strongly absorbs in the near UV, such as melamins. Of course, testing such mechanisms requires the study of the microstructure and

pigment composition of the feathers (Anderson 1999, Prum *et al.* 1999, 2003; Mays *et al.* 2004, Shawkey & Hill 2005, Shawkey *et al.* 2005).

Juvenile males of both species are green, like females, and they achieve their blue color in subsequent molts (Isler & Isler 1999). At least in the Swallow Tanager, acquisition of blue plumage requires four years, and thus the study of the feather microstructural changes and pigment composition throughout the ontogeny may illustrate the physical process underlying the sexual dichromatism of this species.

Endler (1993, 2000) proposed that any visual signal that evolved to maximally stimulate the visual system of a receiver should exhibit a match between its reflectance spectrum and the spectrum of the available environmental light and, simultaneously, maximize the contrast with the background (sensory drive hypothesis). Both studied species, the Swallow Tanager and the Blue Dacnis, inhabit the forest canopy and forest edge, and forage relatively high in trees (Isler & Isler 1999), where light conditions that correspond to woodland shadow and large gaps and are prevalent (Endler 1993, Théry 2006). Under these circumstances, blue and UV coloration would maximize brightness, since they match the most abundant wavelengths in the ambient light (Endler 1993, Gomez & Théry 2004, Théry 2006). Although blue males are probably more conspicuous than green females because of their higher contrast against the green and non UV reflecting background of the forest canopy, those with the described bimodal blue pattern could drastically reduce their conspicuousness by moving into the forest understory, where there are different light conditions (forest shade, Endler 1993). Thus, both sexes should be relatively cryptic in forest shade where, due to the scarcity of UV wavelengths in the ambient light, males could only reflect medium wavelengths similar to

their vegetation background. However, recent work by Endler *et al.* (2005) and Stoddard & Prum (2008) suggests that ambient light would not play an important role on color perception by birds since the visual color constancy correction of their visual system would eliminate any effect of uneven wavelength distribution in the irradiating spectra, minimizing the chances of ambient light to drive the evolution of plumage coloration.

According to the molecular phylogeny of the Thraupidae (Burns 1997, Burns *et al.* 2003) the Swallow Tanager is a sister species in the clade composed with the genera *Dacnis* and *Cyanerpes*. Both, *Dacnis* and *Cyanerpes* comprise several species characterized by green or olive-green females and turquoise, blue and violet males, with the notable exception of the Yellow-bellied *Dacnis* (*D. flaviventris*) that has a predominately yellow plumage. Even though we found interspecific statistical differences in some of the color parameters in some of the analyzed plumage patches, these are minor in comparison with sexual differences among species and do not follow a consistent pattern. Therefore, the marked sexual dichromatism found in both the Swallow Tanager and the Blue *Dacnis* would be most parsimoniously explained as a homologous condition, produced by a similar mechanism in each sex. There are, however, many apparent instances of convergent evolution of blue-green sexual dichromatism among tanagers, for example, such color dimorphism exists in some species of *Tangara*, a genus not closely related to the clade comprised by *Tersina*, *Dacnis* and *Cyanerpes* (Burns 1997). Moreover, blue-green sexual dichromatism is also present in more distantly-related passerine genera, like *Euphonia* and *Chlorophonia*, which are not members of the Thraupidae family (Burns 1997, Burns *et al.* 2003). In addition, the variability in the reflectance spectra shapes of blue plumages reinforces the need of spectrophotometry analysis when dealing

with avian coloration, and suggests that similar patterns to the human eye can be probably generated by different inner mechanisms. Given these facts, it seems interesting to investigate if convergence in this particular and extended sexual dichromatism pattern is also produced by convergent mechanisms.

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