Sexual dichromatism and condition-dependence in the skin of a bat

Bernal Rodríguez-Herrera, Paulina Rodríguez, Whitney Watson, Gary F. McCracken, Rodrigo A. Medellín, and Ismael Galván*

School of Biology, University of Costa Rica, 2060 San José, Costa Rica (BR-H, PR)
Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, CO 80523, USA (WW)
Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, TN 37996, USA (GFM)
Institute of Ecology, Autonomous National University of Mexico, 70-275 Ciudad de México, Mexico (RAM)
Department of Evolutionary Ecology, Doñana Biological Station, CSIC, 41092 Sevilla, Spain (IG)

* Correspondent: galvan@ebd.csic.es

Bats are assumed not to use vision for communication, despite recent evidence of their capacity for color vision. The possibility that bats use color traits as signals has thus been overlooked. Some tent-roosting bats have a potential for visual signaling because they exhibit bright yellow skin, a trait that in birds often acts as a sexual signal. We searched for evidence of sexual dichromatism in the yellow bare skin of Honduran white bats *Ectophylla alba*, the first reported mammal with a capacity to deposit significant amounts of carotenoid pigments in the skin. We found that skin yellow chroma, a measure that reflects carotenoid content, increases in the ears and nose-leaf during development probably due to an increase in dietary carotenoid accumulation. Once in the adulthood, the yellow color of the nose-leaf becomes brighter in males, representing the first evidence of sexual dichromatism in a bat. The nose-leaf brightness tends to covary positively with the body condition of males. We also found that the skin shows a reflectance peak at 530 nm that virtually coincides with the main reflectance peak (540 nm) of the back side of *Heliconia* leaves used as roosts. This suggests that these leaves were selected because of camouflage benefits, and the rich lighting conditions of these roosting places then favored the use of skin coloration as a sexual signal. These findings open a new perspective in the physiological and behavioral ecology of bats in which vision has a more relevant role than previously thought.

Se asume que los murciélagos no usan la visión como canal de comunicación, a pesar de la evidencia reciente de su capacidad de visión en color. La posibilidad de que los murciélagos utilicen rasgos de coloración como señales ha sido por tanto ignorada. Algunos murciélagos que fabrican tiendas con hojas para utilizarlas como dormideros presentan el potencial de señalización visual porque exhiben una brillante piel amarilla, un rasgo que en aves actúa a menudo como una señal sexual. Buscamos evidencia de dicromatismo sexual en la piel desnuda amarilla del murciélago blanco hondureño *Ectophylla alba*, el primer mamífero en el que se ha mostrado la capacidad para depositar cantidades significativas de pigmentos carotenoides en la piel. Encontramos que la saturación de la piel amarilla, una medida que refleja el contenido en carotenoides, aumenta en las orejas y en la nariz en forma de hoja durante el desarrollo, probablemente debido a un incremento en la acumulación de carotenoides de la dieta. Una vez en la edad adulta, el color amarillo de la nariz se hace más brillante en los machos, lo que representa la primera evidencia de dicromatismo sexual en un murciélago. El brillo de la nariz tiende a covariar positivamente con la condición física de los machos. También encontramos que la piel muestra un pico de reflectancia en 530 nm que coincide prácticamente con el principal pico de reflectancia (540 nm) del envés de las hojas de *Heliconia* usadas como dormidero. Esto sugiere que estas hojas fueron seleccionadas debido a beneficios para el camuflaje, y las ricas condiciones de luz de estos lugares de dormidero después favorecieron el uso de la coloración de la piel como señal sexual. Estos resultados abren una nueva perspectiva en la ecología fisiológica y del comportamiento de los murciélagos en la que la visión tiene un papel más relevante que el que se había pensado anteriormente.

Keywords: carotenoid-based color, *Ectophylla alba*, sexual dichromatism, sexual selection, skin coloration, tent-roosting bats

Visual communication is assumed to have a negligible role in the behavior of bats because of their nocturnal habits and echolocation capacity, which are important drivers of their ecology (Dechmann and Safi 2005). Recent findings show, however, that bats present a high diversity of pelage markings that is associated with roosting ecology, suggesting that visual traits may be used in inter- or intraspecific communication (Santana et al. 2011). Furthermore, there is increasing evidence that bats can see colors, as several species have been found to possess retinal pigments that allow color vision (Wang et al. 2004; Zhao et al. 2009). Likewise, other studies have shown that bats can perceive ultraviolet (UV) light (Müller et al. 2009; Gorresen et al. 2015). Thus, it is possible that bats use visual communication in a more significant manner than previously thought, including use of color traits for communication. The role of color in the behavioral ecology of bats remains virtually unexplored.

Some bats (22 out of 1,300 known bat species) use modified leaves as roosts (Rodríguez-Herrera et al. 2007), with 17 of these species (all in the family Phyllostomidae, leaf-nosed bats) living in the Neotropics. A characteristic feature of Neotropical tent-roosting bats belonging to the genera *Ectophylla*, *Dermanura*, *Mesophylla*, *Uroderma*, *Vampyressa*, and *Vampyriscus* is that they exhibit yellow bare skin coloration with varying degrees of intensity in the edges and tragus of their ears and nose-leaf. This bright yellow coloration is rather conspicuous, but its potential function as a visual communication trait has not been the object of attention until recently (Galván et al. 2016). Some tent-roosting bats, like *Ectophylla*, also show an absence of hair pigments that produces a white pelage coloration (Fig. 1A), of as yet unexplored functionality. Neotropical tent-roosting bats therefore represent good models to explore the possible function of color in bat communication. Color traits often have a function in sexual selection as shown in birds, in which the process normally leads to more colorful traits in males than in females (Dale et al. 2015). The yellow bare skin coloration and the white pelage coloration exhibited by tent-roosting bats may be perceived and used in communication between sexes.

Here, we examine the hypothesis that the yellow bare skin coloration of the Honduran white bat, *Ectophylla alba* (Fig. 1A), is a sexually selected trait. Although at this stage we cannot make a direct test of the hypothesis, we can take benefit of the fact that sexual dichromatism is indicative of the action of sexual selection (Heinsohn et al. 2005) and thus obtain evidence in support of or against the hypothesis by comparing skin color expression of males and females. We therefore quantified the expression of the yellow coloration of ears and nose-leaf, predicting that, if it has a role in sexual selection, male bats should exhibit a higher expression than females.

The yellow bare skin coloration of Honduran white bats is due to the deposition of a carotenoid pigment (lutein) in the skin (Galván et al. 2016). Although this is the only mammal reported to have such physiological capacity, examples in birds indicate that sexually selected carotenoid-based skin coloration is expressed in adults but not, or only to a small extent, in juveniles (McDonald 2003; Sarasola et al. 2011). This is probably due to 1) a low acquisition of carotenoids in the diet of juveniles, which leads to low levels of carotenoids in the blood, as animals only obtain carotenoids from the plant products taken as food, or 2) a low expression of certain hormones that mediate the deposition of circulating carotenoids in the integument (Negro et al. 2001). In contrast, carotenoid-based skin color traits that function in other processes such as parent–offspring communication, but not in sexual selection, are expressed by juvenile birds (e.g., Dugas 2009). An increase in the expression of carotenoid-based skin coloration during development therefore seems characteristic of skin color traits that evolve by sexual selection, at least in birds. Thus, we also compared the expression of yellow skin coloration of adult and immature Honduran white bats as a potential second line of evidence for the role of this trait in sexual selection.

Lastly, sexually selected traits are expected to show heightened condition-dependence (Cotton et al. 2004). In the particular case of bare parts of the integument, the expression of carotenoid-based coloration often signals the physical body condition of birds (Iverson and Karubian 2017). We therefore tested whether the expression of yellow skin coloration in Honduran white bats was related to their body condition as a potential third line of evidence that this trait may be under sexual selection. In addition to the yellow skin coloration, we tested the sexual selection hypothesis in the expression of the white pelage coloration of bats.

It is also possible that the yellow skin coloration of Honduran white bats confers cryptic coloration and protection from predators. This is likely, as although appearing conspicuous when perceived isolated from the environment (Fig. 1A), Honduran white bats appear cryptic when observed in the abaxial (back) side of the *Heliconia* leaves where they roost (Fig. 1B). We therefore obtained the reflectance spectra of upper and back sides of a *Heliconia* leaf used as a communal roost and compared them to the spectra of the yellow skin coloration of Honduran white bats. As these bats mainly use *Heliconia* leaves to roost (Rodríguez-Herrera et al. 2008), if such specific roosting selection responds to the adaptive benefits of camouflage, then the reflectance spectra of leaves should resemble those of the yellow skin of bats.

MATERIALS AND METHODS

Field methods.—Fieldwork was conducted in October 2017 mainly in the Tirimbina Biological Reserve (TBR; 10°26′N, 83°59′W), on the Northeastern Caribbean lowlands of Costa Rica. Additional data were collected from private gardens in the Sarapiquí River Basin region. TBR is between 40 and 150 m a.s.l. and is comprised of tropical wet forest (Holdridge 1967).

Honduran white bats were captured during the day directly from their tents with specific traps designed by one of the coauthors of this study (BR-H). After capture, bats were placed in individual cloth bags and transported to the main facilities at TBR, where measurements were taken. In total, we captured 27 adults (16 males and 11 females) and nine immatures (four males and five females), plus one young individual still being

Fig. 1.—Images of the face of a Honduran white bat (*Ectophylla alba*; A) and a group of Honduran white bats roosting in a *Heliconia* leaf modified to be used as a tent (B). Photo credits: Bernal Rodríguez-Herrera.

nourished by lactation. Immatures were differentiated from adults on the basis of a smaller forearm (< 28 mm).

We measured the body mass of bats to the nearest 0.5 g with a Pesola AG (Schindellegi, Switzerland) balance, and the forearm length with a ruler as a measure of body size. We could not measure the body mass of one adult male. The physical body condition of bats was calculated as the residuals of $\log_{10}$ body mass regressed against $\log_{10}$ forearm length (Entwistle et al. 1998). Research on live animals followed ASM guidelines (Sikes et al. 2016).

Analysis of skin color expression.—We analyzed the color expression of the yellow skin of Honduran white bats using an Ocean Optics Jaz spectrophotometer (range 220–1,000 nm) with UV (deuterium) and visible (tungsten-halogen) lamps and a bifurcated 400 µm fiber optic probe. The fiber optic probe both provided illumination and obtained light reflected from the sample, with a reading area of ca. 1 mm^2. Measurements were taken at a 90° angle to the yellow bare skin of ears and nose-leaf or to the white dorsal pelage. All measurements were relative to a diffuse reflectance standard tablet (WS-1; Ocean

Optics, Dunedin, Florida), and reference measurements were made frequently. An average spectrum of two readings on different points of each ear, two readings on different points of the nose-leaf, and two readings on different points of the dorsal pelage, was obtained for each bat, removing the probe after each measurement. Similar measurements were made on one of the *Heliconia* leaves from which Honduran white bats were captured, calculating an average spectrum of six readings on different points of the upper or back side of the leaf. Reflectance curves were determined by calculating the median of the percent reflectance in 10-nm intervals.

The bare skin of Honduran white bats displayed the same shape of reflectance spectra as reported for yellow and orange carotenoid-pigmented integumentary parts in other animals (Baldwin and Johnsen 2012). These spectra thus present a peak in the UV (300–400 nm) and two peaks in the green and red spectral regions (530 and 630 nm; Figs. 2 and 3), which results in the perception of yellow color (Fig. 1). We therefore summarized reflectance data of the yellow skin as the summed reflectance across the yellow range ($R_{530-630}$; yellow brightness), and also as the contribution of reflectance across the yellow range to total reflectance across the visible range ($R_{530-630}/R_{400-700}$; yellow chroma—Saks et al. 2003). We also calculated these measures in relation to the UV spectral range and total reflectance (UV brightness: $R_{300-400}$; UV chroma: $R_{300-400}/R_{300-700}$). Lastly, white is by definition uniform reflectance across all wavelengths, thus we summarized reflectance data of the white pelage, whose reflectance spectra show no significant peaks (Fig. 4), as the summed reflectance across the entire spectral range ($R_{300-700}$).

Statistical analyses.—We used general linear models (GLM) to test the effects of sex and age on the color expression of Honduran white bats, with each color trait as a response variable and sex, age, and their interaction as fixed predictor terms.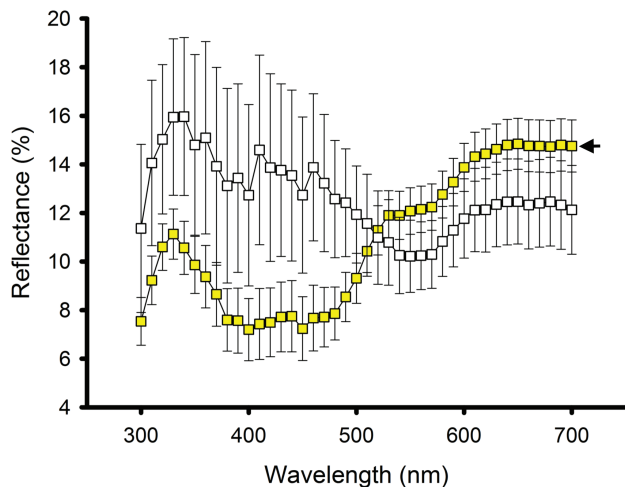 When the effect of the interaction between sex and age was significant, we explored differences between groups by means of Fisher LSD post hoc tests. Nonsignificant terms were removed from the models starting with the interaction. The exploration of the distribution of residuals from the models confirmed that normality assumptions were fulfilled. We tested the association between body condition and the color trait that was sexually dichromatic (see "Results") by means of Pearson's correlation tests for males and females separately.

RESULTS

Sex- and age-related effects on color expression.—The mean values of the different color traits measured in the skin of Honduran white bats are shown in Table 1. The brightness of the yellow skin of the ears of Honduran white bats did not
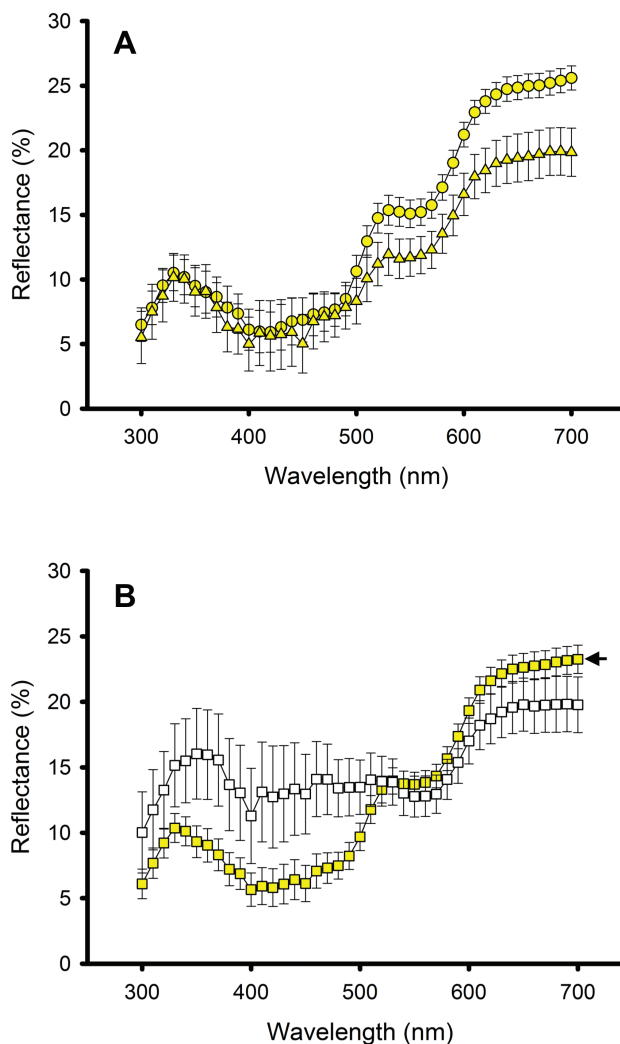

Fig. 2.—Spectral reflectance (± *SE*) of the yellow skin of the ears of adult (yellow squares; indicated by an arrow) and immature (white squares) Honduran white bats (*Ectophylla alba*). Data are provided in 10-nm intervals. Ultraviolet (UV) range: 300–400 nm. Visible range: 400–700 nm.

Fig. 3.—Spectral reflectance (± *SE*) of the yellow skin of the nose-leaf of Honduran white bats (*Ectophylla alba*). (A) Reflectance spectra for adult males (circles) and females (triangles). (B) Reflectance spectra for adults (yellow squares; indicated by an arrow) and immatures (white squares), with data for males and females pooled in each category. Data are provided in 10-nm intervals. Ultraviolet (UV) range: 300–400 nm. Visible range: 400–700 nm.

depend on either sex ($F_{1,34} = 1.52$, $P = 0.226$), age ($F_{1,33} = 0.70$, $P = 0.409$), or their interaction ($F_{1,32} = 1.83$, $P = 0.185$). The yellow chroma of the ears, however, depended on age ($F_{1,34} = 5.59$, $P = 0.024$), but not on sex ($F_{1,33} = 0.07$, $P = 0.785$) nor its interaction with age ($F_{1,32} = 0.18$, $P = 0.676$). The age effect was due to adult bats having higher chroma values in the ears (mean ± *SE*: 0.42 ± 0.01) than immature bats (0.35 ± 0.03; Fig. 2). The UV reflectance of ears did not depend on sex or age, either regarding UV brightness (all *P*-values > 0.09) or UV chroma (all *P*-values > 0.148).

The brightness of the yellow skin of the nose-leaf showed a significant interaction between sex and age ($F_{1,32} = 5.93$, $P = 0.021$), due to a difference in brightness between males and females among adults ($P = 0.032$) but not among immatures ($P = 0.140$). The brightness of the nose-leaf of adult males (205.10 ± 12.91) was thus higher than that of adult females (159.89 ± 15.58; Fig. 3A). There was also a significant difference in the brightness of the nose-leaf of adult versus immature males ($P = 0.028$), with the latter showing lower values (138.88 ± 25.83). The yellow chroma of the nose-leaf, on the other hand, followed the same pattern as the ears, with a significant effect of age ($F_{1,34} = 5.36$, $P = 0.027$) due to higher values

Fig. 4.—Spectral reflectance (± *SE*) of the skin of the nose-leaf (yellow circles; indicated by an arrow) and ears (white circles) of a young Honduran white bat (*Ectophylla alba*) still nourished by lactation. Data are provided in 10-nm intervals. Ultraviolet (UV) range: 300–400 nm. Visible range: 400–700 nm.

in adults (0.43 ± 0.01) than in immatures (0.37 ± 0.03; Fig. 3B), and nonsignificant effects of sex ($F_{1,33} = 0.07$, $P = 0.793$) and their interaction with age ($F_{1,32} = 5.36$, $P = 0.794$). Also similar to the ears, the UV chroma of the nose-leaf did not depend on sex or age (all *P*-values > 0.214), although the effect of age on UV brightness was only marginally nonsignificant ($F_{1,34} = 4.12$, $P = 0.050$), with a tendency of immature bats to have higher UV brightness (139.98 ± 23.79) than adults (84.19 ± 13.74; Fig. 3B).

The reflectance spectra of the young Honduran white bat nourished by lactation that we examined showed a similar shape to the spectra of adult and immature bats in the nose-leaf, but with lower reflectance values overall and the peak at 530 nm slightly displaced to shorter wavelengths (Fig. 4). The reflectance spectra of the ears of the young bat was, however, almost flat and showed very low reflectance values (Fig. 4), being indicative of a whitish color.

Lastly, the reflectance spectra of the white pelage of bats did not show variation between sexes or ages (Fig. 5). Thus, the summed reflectance values for the white pelage had no significant effects of age ($F_{1,34} = 1.99$, $P = 0.168$), sex ($F_{1,33} = 1.46$, $P = 0.236$), or their interaction ($F_{1,32} = 1.63$, $P = 0.210$).

Effect of body condition on color expression.—The brightness of the yellow skin of the nose-leaf, which was the sexually dichromatic trait, was not correlated with body condition for males ($r = 0.08$, $n = 19$, $P = 0.750$) or for females ($r = −0.07$, $n = 16$, $P = 0.801$; Fig. 6). However, when two apparent outliers that were males with high brightness values and the poorest body conditions were removed from the analysis (Fig. 6), the correlation became significant ($r = 0.53$, $n = 17$, $P = 0.028$). Thus, the brightness of the nose-leaf tended to increase with the body condition of male Honduran white bats.

Reflectance of roost leaves.—The measured *Heliconia* leaf that was being used by Honduran white bats as a roost showed contrasted reflectance spectra in the upper and back sides. The spectra of both sides showed two reflectance peaks, one in the blue spectral region (430 nm) and another in the green spectral region (540 nm; Fig. 7) that virtually coincides with the peak at 530 nm observed in the reflectance spectra of the yellow skin of bats (Figs. 2 and 3). It is the presence of both peaks that probably makes that the color of these leaves to be perceived as green (Fig. 1B). However, while the blue spectral peak predominates in the upper side of the leaf, the green peak predominates in the back side (Fig. 7). This means that
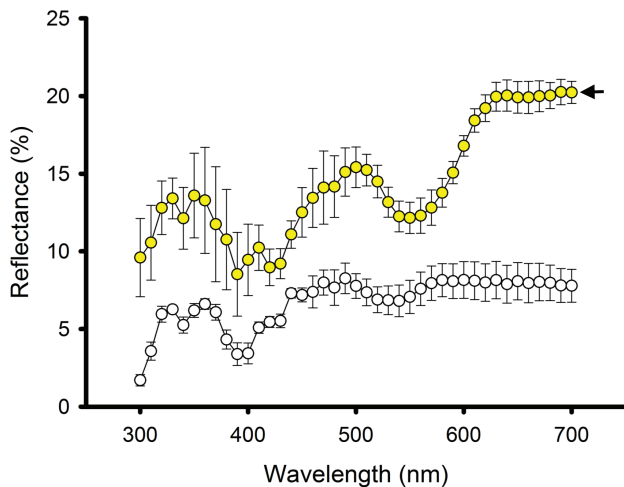
Table 1.—Mean (± *SE*) values for the color traits measured in the yellow skin of ears and nose-leaf of Honduran white bats (*Ectophylla alba*) of different sexes and age classes. UV = ultraviolet.

Color trait	Adults				Immatures			
	Males		Females		Males		Females	
	Ears	Nose-leaf	Ears	Nose-leaf	Ears	Nose-leaf	Ears	Nose-leaf
Yellow brightness	158.15 ± 14.01	205.10 ± 10.78	122.39 ± 14.43	159.89 ± 17.11	109.86 ± 7.52	138.88 ± 20.79	132.22 ± 29.33	191.38 ± 23.07
Yellow chroma	0.42 ± 0.02	0.42 ± 0.01	0.42 ± 0.02	0.42 ± 0.02	0.33 ± 0.04	0.37 ± 0.05	0.36 ± 0.04	0.36 ± 0.02
UV brightness	87.80 ± 12.52	86.83 ± 14.03	98.39 ± 19.43	80.34 ± 17.94	150.68 ± 65.88	101.13 ± 52.73	136.44 ± 35.65	171.06 ± 33.60
UV chroma	0.18 ± 0.02	0.14 ± 0.02	0.23 ± 0.03	0.17 ± 0.03	0.23 ± 0.07	0.14 ± 0.08	0.27 ± 0.03	0.22 ± 0.02

the back side of *Heliconia* leaves is more greenish-yellowish, while the upper side is more bluish. Thus, the spectral peak at the green region for the skin of Honduran white bats coincides with the predominant peak of the back side of the leaves where they roost.
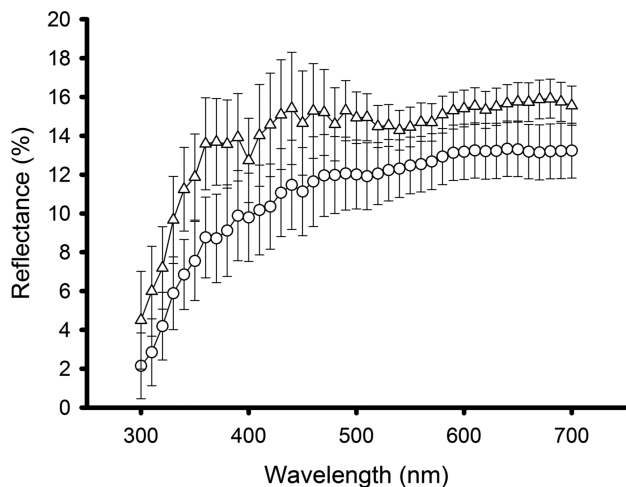

Fig. 5.—Spectral reflectance (± *SE*) of the white pelage of male (circles) and female (triangles) Honduran white bats (*Ectophylla alba*). Data are provided in 10-nm intervals. Ultraviolet (UV) range: 300–400 nm. Visible range: 400–700 nm.

DISCUSSION

Our study opens a new perspective in the physiological and behavioral ecology of bats by showing that at least tent-roosting species probably use color traits in intraspecific communication. Sexual dichromatism in the nose-leaf of Honduran white bats is supported, as males showed brighter yellow nose-leaves than females. Sexual dichromatism is known to result from the action of sexual selection exerted by one sex, normally females, resulting in more colorful traits in males (Heinsohn et al. 2005; Dale et al. 2015). Honduran white bats displayed sexual dichromatism in the skin of the nose-leaf but not in the skin of ears, which also is yellow. The nose-leaf of phyllostomid bats confers benefits for foraging and orientation (Bogdanowicz et al. 1997), and the nose-leaf has evolved as a prominent morphological structure in the face of bats. This prominence may have favored the evolution of a secondary sexual signaling function in the nose-leaf (Irschick et al. 2007). Indeed, extraordinarily large nose structures that have evolved by natural selection have also secondarily evolved as sexual signals in other mammals like the saiga (*Saiga tatarica*—Frey et al. 2007), the proboscis monkey (*Nasalis larvatus*—Murai 2006), and even humans (Mikalsen et al. 2014).

The effect of age also supports the role of sexual selection in the skin coloration of Honduran white bats. The yellow chroma of both ears and nose-leaf increased during the development of bats, as revealed by higher values in adults than in immatures.
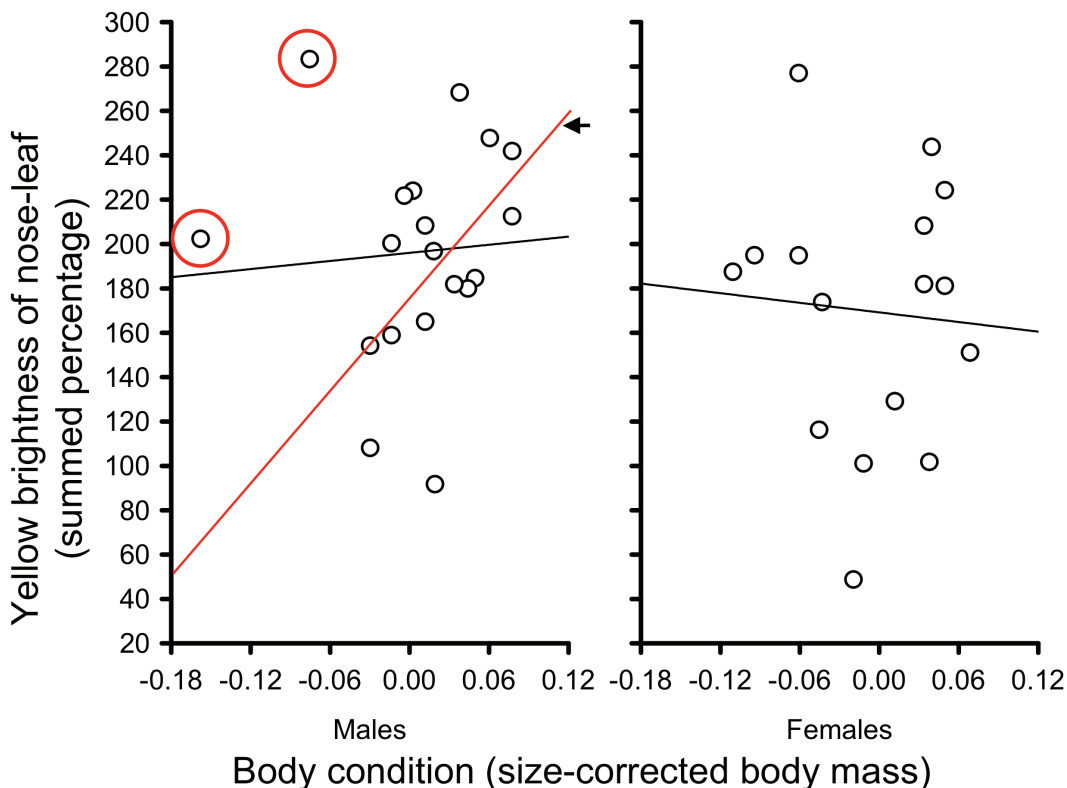

Fig. 6.—Relationship between the brightness of the yellow skin of the nose-leaf (summed percentage in the spectral region that is perceived as yellow) and body condition (residuals of body mass regressed against forearm size) in male and female Honduran white bats (*Ectophylla alba*). Black lines are regression lines including all points. Two outliers are marked with circles in the graph for males; the line indicated by an arrow is the regression line excluding these outliers.
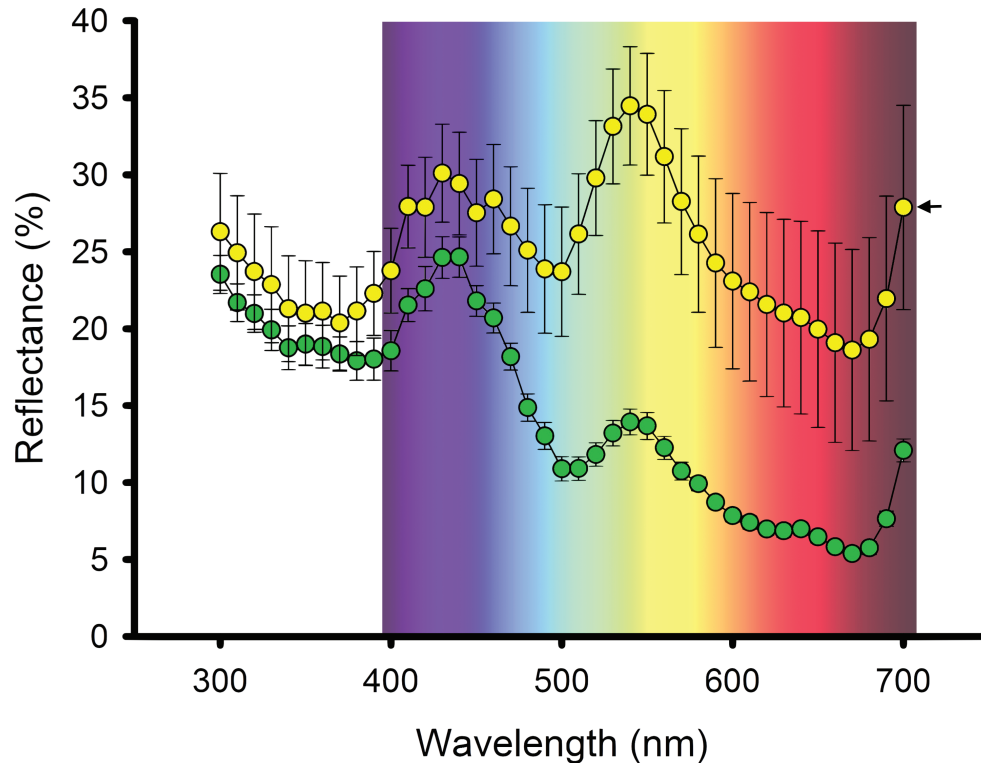
Fig. 7.—Spectral reflectance (± *SE*) of the upper (green circles) and back (yellow circles, indicated by an arrow) sides of a *Heliconia* leaf modified by Honduran white bats (*Ectophylla alba*) to be used as a roosting tent. Data are provided in 10-nm intervals. The colors of the visible spectrum are depicted behind the graph. Note that the main reflectance peak of the back side is located in the yellow spectral region, while the main peak of the upper side is located in the blue region.

This means that the skin becomes yellower during development, probably as a consequence of an accumulation of carotenoids, as chroma reflects carotenoid content in integumentary structures colored by these pigments (Saks et al. 2003). Immature Honduran white bats progressively abandon the lactating diet and increase consuming ripe red fruits of the fig tree *Ficus colubrinae*, which represents the only food item of this species (Rodríguez-Herrera et al. 2007) and is thus the source of carotenoids that color the skin (Galván et al. 2016). The only young bat still nourished by lactation examined showed whitish skin in the ears and a diminished expression of yellow color in the nose-leaf, suggesting that the accumulation of skin carotenoids begins in the sexually dichromatic feature (i.e., nose-leaf) and then expands to other structures until adulthood. In birds, for which the role of carotenoid-based coloration in sexual selection has more intensively been investigated, the expression of color in yellow bare parts that function as sexual signals often follows a similar pattern of increasing during development (McDonald 2003; Sarasola et al. 2011). This lends additional support to a potential role of the yellow skin coloration of Honduran white bats as a visual sexual signal.

On the other hand, the brightness of the yellow nose-leaf, which was sexually dichromatic, also was positively associated with the body condition of males, which also suggests a role for skin coloration in sexual selection (Cotton et al. 2004). Although the dependence of skin brightness on body condition relied on the removal of two outlier points associated with extreme values, the pattern of relationship was clearly different in

male versus female bats (see Fig. 6). The fact that the association arose after the removal of outliers and was only present in males is consistent with a role of this sexually dichromatic trait in sexual selection, which is normally exerted by females and thus leads to more ornamented males, as first noted by Darwin (1871). In the particular case of carotenoid-based coloration, the association with body condition can be explained because carotenoids act as important antioxidants and immunostimulants but cannot fulfill these functions when deposited in the integument, and thus only individuals in good condition may be able to allocate large amounts of carotenoid resources to pigmentation (Olson and Owens 1998). This hypothesis is supported by studies on bare parts colored by carotenoids in birds (Biard et al. 2010; Vergara and Fargallo 2011; Blévin et al. 2014), which also show that carotenoid-based coloration generally signals the performance of antioxidant and immune functions (Blount et al. 2003; McGraw and Ardia 2003; Alonso-Alvarez et al. 2004; Peters et al. 2004; Alonso-Alvarez and Galván 2011). Female birds can thus maximize their fitness prospects by selecting males with a high expression of carotenoid-based integument coloration (Velando et al. 2006). This may also explain the condition-dependence of the yellow coloration of the nose-leaf in male Honduran white bats and the evolution of this trait as a sexual signal. It seems, however, that some proportion of variance in the brightness of the yellow nose-leaf is not explained by body condition (Fig. 6), suggesting that other factors might also be affecting the color of the nose-leaf. For example, Honduran white bats could have

evolved a physiological mechanism related to individual quality on which the expression of yellow skin coloration depends, as recently found in the expression of melanin-based coloration in birds (Galván and Alonso-Alvarez 2017). This will have to be investigated by future studies.

To summarize, the skin of the ears and the nose-leaf of Honduran white bats becomes yellower during development, and once in adulthood, the yellow skin of the nose-leaf of males becomes brighter than that of females. The brightness of the nose-leaf also covaries positively with the body condition of males, thus suggesting the possibility for sexual selection by females. Vision has traditionally been assumed to have a minor importance in the communication of bats, but Santana et al. (2011) showed that their high diversity in pelage markings is associated with roosting ecology and thus has a high potential for visual communication. Our findings in the Honduran white bat indicate that these bats probably use color traits of skin pigmentation in intraspecific communication, and provide evidence suggesting a role for sexual selection. Tent-roosting bats are usually exposed to more illuminated conditions than other bats that roost in caves or hollow trees, which may have favored the evolution of colored skin in species such as the Honduran white bat, similar to the effect of ambient light on the evolution of plumage coloration in Neotropical rainforest birds (Gómez and Théry 2004). Communal roosting may have also contributed to a signaling function of colored skin, as gregarious behavior is known to promote the evolution of such traits (Leo Lester et al. 2005).

However, the potential for visual communication may not have been the primary driver of the evolution of colored skin in the Honduran white bat. We found that the back side of *Heliconia* leaves where the bats roost has a reflectance peak at 540 nm that virtually coincides with the peak at 530 nm found in the yellow skin of bats. This coincidence of reflectance peaks does not occur in the upper side of the same leaves. As a result, the yellow skin color of Honduran white bats is not perceived from below when the bats are roosting inside tents (see Fig. 1B; Rodríguez-Herrera et al. 2007). A likely scenario during the evolutionary history of Honduran white bats is therefore as follows: 1) the adoption of a diet highly specialized in *F. colubrinae* fruits increased the accumulation of carotenoids in the skin and thus generated a yellow coloration; 2) natural selection favored the selection of the back side of *Heliconia* leaves as roosting places by bats because the resemblance of the yellow coloration with the color of leaves confers camouflage; and 3) the rich ambient light inside tents and the communal roosting behavior favored the use of the nose-leaf skin color of males as a mate choice criterion by females. The entire process may have favored Honduran white bats to esterify lutein with fatty acids (i.e., lutein bonds to a fatty acid in a condensation reaction and gives a single compound), as this probably creates a permanent skin coloration (Galván et al. 2016). Although the selection of *Heliconia* leaves as roosting places has additional thermal benefits for bats (Rodríguez-Herrera et al. 2016), that the benefits of camouflage have contributed to this selection is supported by the white pelage coloration of Honduran white bats. Given the apparent incapacity of mammals to deposit carotenoids in hairs, depigmented pelage creating uniform reflectance of light (see Fig. 6) seems a better evolutionary solution to achieve camouflage against leaves than if it was colored by the only pigments that mammals can deposit in hairs (i.e., melanins—Galván and Wakamatsu 2016). Indeed, we did not find any sex or age effect on the white color expression of the pelage of Honduran white bats, precluding any effect of sexual selection on this trait.

Despite it probably not being the main driver of the evolution of colored skin, our findings suggest that the capacity of visual communication of bats has been undervalued. Bats, however, possess retinal pigments that allow the perception of long-wavelength light (Zhao et al. 2009), and also can perceive UV light (Müller et al. 2009; Gorresen et al. 2015). In this regard, we note a tendency in immature Honduran white bats to show a higher UV brightness in the nose-leaf (i.e., the potentially signaling trait) than adults. Interestingly, the UV component of carotenoid-based coloration, which is not generated by the pigments but by the integumentary structure on which they are deposited, is used in some birds by parents to make decisions when feeding their offspring (Galván et al. 2008). Although the immature Honduran white bats examined in our study were weaned, they may still depend on parents (Rodríguez-Herrera et al. 2007). Future studies should explore the possibility that the UV component of the nose-leaf skin of immature Honduran white bats also serves as a signal in parent–offspring communication.

Acknowledgments

Literature Cited

Alonso-Alvarez, C., and I. Galván. 2011. Free radical exposure creates paler carotenoid-based ornaments: a possible interaction in the expression of black and red traits. PLoS One 6:e19403.

Alonso-Alvarez, C., et al. 2004. An experimental test of the dose-dependent effect of carotenoids and immune activation on sexual signals and antioxidant activity. American Naturalist 164:651–659.

Baldwin, J., and S. Johnsen. 2012. The male blue crab, *Callinectes sapidus*, uses both chromatic and achromatic cues during mate choice. Journal of Experimental Biology 215:1184–1191.

Biard, C., N. Saulnier, M. Gaillard, and J. Moreau. 2010. Carotenoid-based bill colour is an integrative signal of multiple parasite infection in blackbird. Naturwissenschaften 97:987–995.

Blévin, P., et al. 2014. Integument colouration in relation to persistent organic pollutants and body condition in arctic breeding black-legged kittiwakes (*Rissa tridactyla*). Science of the Total Environment 470:248–254.

Blount, J. D., N. B. Metcalfe, T. R. Birkhead, and P. F. Surai. 2003. Carotenoid modulation of immune function and sexual attractiveness in zebra finches. Science 300:125–127.

Bogdanowicz, W., R. D. Csada, and M. B. Fenton. 1997. Structure of noseleaf, echolocation, and foraging behavior in the Phyllostomidae (Chiroptera). Journal of Mammalogy 78:942–953.

Cotton, S., K. Fowler, and A. Pomiankowski. 2004. Do sexual ornaments demonstrate heightened condition-dependent expression as predicted by the handicap hypothesis? Proceedings of the Royal Society of London, B. Biological Sciences 271:771–783.

Dale, J., C. J. Dey, K. Delhey, B. Kempenaers, and M. Valcu. 2015. The effects of life history and sexual selection on male and female plumage colouration. Nature 527:367–370.

Darwin, C. 1871. The descent of man and selection in relation to sex. John Murray, London, United Kingdom.

Dechmann, D. K. N., and K. Safi. 2005. Studying communication in bats. Cognition, Brain, Behavior 9:479–496.

Dugas, M. B. 2009. House sparrow, *Passer domesticus*, parents preferentially feed nestlings with mouth colours that appear carotenoid-rich. Animal Behaviour 78:767–772.

Entwistle, A. C., P. A. Racey, and J. R. Speakman. 1998. The reproductive cycle and determination of sexual maturity in male brown long-eared bats, *Plecotus auritus* (Chiroptera: Vespertilionidae). Journal of Zoology 244:63–70.

Frey, R., I. Volodin, and E. Volodina. 2007. A nose that roars: anatomical specializations and behavioural features of rutting male saiga. Journal of Anatomy 211:717–736.

Galván, I., and C. Alonso-Alvarez. 2017. Individual quality via sensitivity to cysteine availability in a melanin-based honest signaling system. Journal of Experimental Biology 220:2825–2833.

Galván, I., L. Amo, and J. J. Sanz. 2008. Ultraviolet-blue reflectance of some nestling plumage patches mediates parental favouritism in great tits *Parus major*. Journal of Avian Biology 39:277–282.

Galván, I., J. Garrido-Fernández, J. Ríos, A. Pérez-Gálvez, B. Rodríguez-Herrera, and J. J. Negro. 2016. Tropical bat as mammalian model for skin carotenoid metabolism. Proceedings of the National Academy of Sciences of the United States of America 113:10932–10937.

Galván, I., and K. Wakamatsu. 2016. Color measurement of the animal integument predicts the content of specific melanin forms. RSC Advances 6:79135–79142.

Gómez, D., and M. Théry. 2004. Influence of ambient light on the evolution of colour signals: comparative analysis of a Neotropical rainforest bird community. Ecology Letters 7:279–284.

Gorresen, P. M., P. M. Cryan, D. C. Dalton, S. Wolf, and F. J. Bonaccorso. 2015. Ultraviolet vision may be widespread in bats. Acta Chiropterologica 17:193–198.

Heinsohn, R., S. Legge, and J. A. Endler. 2005. Extreme reversed sexual dichromatism in a bird without sex role reversal. Science 309:617–619.

Holdridge, L. R. 1967. Life zone ecology (revised edn). Tropical Science Centre, San José, Costa Rica.

Irschick, D. J., A. Herrel, B. Vanhooydonck, and R. Van Damme. 2007. A functional approach to sexual selection. Functional Ecology 21:621–626.

Iverson, E. N., and J. Karubian. 2017. The role of bare parts in avian signaling. Auk 134:587–611.

Leo Lester, R., C. Grach, M. Paul Pener, and S. J. Simpson. 2005. Stimuli inducing gregarious colouration and behaviour in nymphs of *Schistocerca gregaria*. Journal of Insect Physiology 51:737–747.

McDonald, P. G. 2003. Variable plumage and bare part colouration in the Brown Falcon, *Falco berigora*: the influence of age and sex. Emu 103:21–28.

McGraw, K. J., and D. R. Ardia. 2003. Carotenoids, immunocompetence, and the information content of sexual colors: an experimental test. American Naturalist 162:704–712.

Mikalsen, Å. K. R., I. Folstad, N. G. Yoccoz, and B. Laeng. 2014. The spectacular human nose: an amplifier of individual quality? PeerJ 2:e357.

Müller, B., M. Glösmann, L. Peichl, G. C. Knop, C. Hagemann, and J. Ammermüller. 2009. Bat eyes have ultraviolet-sensitive cone photoreceptors. PLoS One 4:e6390.

Murai, T. 2006. Mating behaviors of the proboscis monkey (*Nasalis larvatus*). American Journal of Primatology 68:832–837.

Negro, J. J., J. L. Tella, F. Hiraldo, G. R. Bortolotti, and P. Prieto. 2001. Sex-and age-related variation in plasma carotenoids despite a constant diet in the red-legged partridge *Alectoris rufa*. Ardea 89:275–280.

Olson, V. A., and I. P. Owens. 1998. Costly sexual signals: are carotenoids rare, risky or required? Trends in Ecology & Evolution 13:510–514.

Peters, A., A. G. Denk, K. Delhey, and B. Kempenaers. 2004. Carotenoid-based bill colour as an indicator of immunocompetence and sperm performance in male mallards. Journal of Evolutionary Biology 17:1111–1120.

Rodríguez-Herrera, B., R. A. Medellín, and M. Gamba-Rios. 2008. Roosting requirements of white tent-making bat *Ectophylla alba* (Chiroptera: Phyllostomidae). Acta Chiropterologica 10:89–95.

Rodríguez-Herrera, B., R. A. Medellín, and R. M. Timm. 2007. Neotropical tent-roosting bats. Instituto de Biodiversidad, Santo Domingo, Costa Rica.

Rodríguez-Herrera, B., R. L. Víquez, E. Cordero-Schmidt, J. M. Sandoval, and A. Rodríguez-Durán. 2016. Energetics of tent roosting in bats: the case of *Ectophylla alba* and *Uroderma bilobatum* (Chiroptera: Phyllostomidae). Journal of Mammalogy 97:246–252.

Saks, L., K. J. McGraw, and P. Hõrak. 2003. How feather colour reflects its carotenoid content. Functional Ecology 17:555–561.

Santana, S. E., T. O. Dial, T. P. Eiting, and M. E. Alfaro. 2011. Roosting ecology and the evolution of pelage markings in bats. PLoS One 6:e25845.

Sarasola, J. H., J. J. Negro, M. J. Bechard, and A. Lanusse. 2011. Not as similar as thought: sexual dichromatism in Chimango Caracaras is expressed in the exposed skin but not in the plumage. Journal of Ornithology 152:473–479.

Sikes, R. S., and The Animal Care and Use Committee of the American Society of Mammalogists. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. Journal of Mammalogy 97:663–688.

Velando, A., R. Beamonte-Barrientos, and R. Torres. 2006. Pigment-based skin colour in the blue-footed booby: an honest signal of current condition used by females to adjust reproductive investment. Oecologia 149:535–542.

Vergara, P., and J. A. Fargallo. 2011. Multiple coloured ornaments in male common kestrels: different mechanisms to convey quality. Naturwissenschaften 98:289–298.

Wang, D., et al. 2004. Molecular evolution of bat color vision genes. Molecular Biology and Evolution 21:295–302.

Zhao, H., S. J. Rossiter, E. C. Teeling, C. Li, J. A. Cotton, and S. Zhang. 2009. The evolution of color vision in nocturnal mammals. Proceedings of the National Academy of Sciences of the United States of America 106:8980–8985.