Characterization of the sexual dimorphism in oilbirds (*Steatornis caripensis*)

Andrés Felipe Robayo Salek

Universidad del Rosario
Facultad de Ciencias Naturales
Bogotá, Colombia
2022

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Tesis presentada como requisito para obtener el título de:

Biólogo

Directora

Adriana A. Maldonado-Chaparro

Facultad de Ciencias Naturales
Biología
Universidad del Rosario
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2022

Abstract

The extent to which males and females of monomorphic species differ from each other is still an ecological and evolutionary puzzle. In these species it has been proposed that slight differences in selection pressures can result in phenotypic differences between sexes. However, such differences may be very subtle or may be exhibited in traits that are not perceived by humans, such as coloration. For example, in blue tits (*Cyanistes caeruleus*) males differ from females in the UV reflection of the crown patch. Here, I aimed to identify the morphological differences between sexes in a monomorphic specie, the oilbird (*Steatornis caripensis*). In this species, males are slightly larger and grayish than females, making it difficult to determine the sex of individuals by means other than molecular sexing, an invasive technique. To characterize phenotypic differences between males and females, I measured five morphological traits on 75 museum individuals and 16 wild individuals, and the feather coloration in 33 museum individuals and 11 wild individuals. I used these measures to quantify the degree of sexual dimorphism and identify the traits that differentiate males from females. I found that *S. caripensis* is mostly monomorphic showing subtle differences in the width and the length of the bill, which is larger in males compared to females. I also found subtle differences in plumage coloration suggesting that color may play an important role in the differentiation of the sexes, and possibly in mate choice. My results indicate that despite the slight differences in beak shape between males and females, the sexes in oilbirds seem to be indistinguishable.

Keywords

Sexual selection, Monomorphic species, Molecular sexing

Introduction

The degree of sexual dimorphism, or the systematic differences in phenotypic characteristics between males and females of the same species (Amadon, 1959; Geber et al., 1999), varies widely among species and can be expressed in morphological (Morales et al., 2020), chromatic (Lind & Delhey, 2015), physiological (Lande, 1980), and behavioral (Shine, 1989) traits. These phenotypic differences between sexes can be extreme, for example in peacocks (*Pavo cristatus*), hooded siskin (*Spinus magellanicus*) and zebra finches (*Taeniopygia guttata*), where males have exuberant coloration compared to females (Loyau et al., 2005; Montalti et al., 2004; Birkhead, 1998). Although marked sexual dimorphism is common in nature, there are also species in which the phenotypic differences between males and females are subtle and the sexes are practically indistinguishable. However, to date, most studies on sexual dimorphism have focused on species with marked differences (Biagolini-Jr & Perrella, 2020; Dunn et al., 2001; Hedrick & Temeles, 1989) and it is only until recently that attention has been drawn to understanding the extent to which phenotypic traits vary in species with subtle sexual dimorphism (Diniz et al., 2016; Jones & Hunter, 1993; Morales et al., 2020).

The slight differences among males and females in species with subtle sexual dimorphism can be explained by three hypotheses: 1) the genetic correlation hypothesis (Badyaev & Hill, 2003; Kimball & Ligon, 1999) states that the same trait is represented in the sexes among the same species; 2) the mutual selection hypothesis states that both males and females are the ones who choose their mates (Jones & Hunter, 1993), and 3) the indistinguishable hypothesis states that there is not differentiation between the sexes in the species, as adaptation to avoid competition in flock and colony living species (Burley, 1981). The last hypothesis has been strongly criticized because slight differences in sexual selection pressures between the sexes can result in small differences in sexual characteristics (Andersson et al., 1998a; Björklund, 1984; Diniz et al., 2016; Morales et al., 2020; Van Rooij & Griffith, 2010). Therefore, in species where the sexes are apparently monomorphic, might be small phenotypic differences that characterize and differentiate males and females. However, identifying those traits that vary between sexes is a challenging task as it requires evaluating various traits ranging from morphological to physiological aspects.

Differences in morphological, chromatic, and behavioral traits may be related to differences in ecological and evolutionary processes. For example, in the woodpecker (*Melanerpes striatus*) males have a lengthier bill than females which allows him to be more efficient finding, cracking and eating food, resulting in a sex-related difference in their foraging strategies (Selander, 1966). Additionally, birds are tetrachromatic and sensitive to ultraviolet light (300–400nm) (Bennett et al., 1994), thus color that is imperceptible to the human eye can also be a source of sexual dimorphism. For example, in the Eurasian blue tit *(Cyanistes caeruleus)* reflectance measures showed that males have stronger UV and UV/violet chroma than females, which may play a role in mate acquisition (Andersson et al., 1998b). These chromatic differences can also be present in nocturnal birds, which can detect UV light (Höglund et al., 2019), and therefore are able to see the UV-reflection of feathers at night (Martin et al., 2007). For example, in the eared dove (*Zenaida auriculata*), a study based on a visual model, found differences in achromatic and chromatic levels between the crowns of males and females, a difference possibly involved in sexual selection (Valdez & Benitez-Vieyra, 2016).

In this study I will characterize the phenotypic differences in morphometric and plumage color traits between males and females in oilbirds (*Steatornis caripensis*), and determine if these differences are sufficient to discriminate between the sexes. Understanding the phenotypic differences between males and females in this species allows us to hypothesize about their mating system and the evolutionary pressures (i.e., natural selection and sexual selection) that gave rise to this pattern of dimorphism(Amadon, 1959; Dale et al., 2007; Lande, 1980; MacArthur, 1972; Shine, 1989).

Materials and methods

Study species

S. caripensis is the only species of the Steatornithidae family. It is a nocturnal bird species (Lind & Delhey, 2015), strictly frugivorous (Martin et al., 2004), and fulfills an ecological function as a seed disperser (Holland et al., 2009). It is hypothesized that have a monogamous mating system (Cleere & Nurney, 1998), and show a subtle sexual dimorphism , with males slightly larger and grayish than females (Hilty & Brown, 1986).

For this study I used museum individuals from seven ornithological collections in the Americas, and wild individuals from two locations in Santander, Colombia. Birds were captured at two caves in the towns of El Peñon, and Bolivar, using 6 meters or 9 meters long mist nets placed at the entrance of the caves. The nets were opened between 18:00 and 20:00 hours and checked every half hour.

Phenotypic characterization of museum individuals

To characterize the phenotypic differences between males and females I measured morphological traits on individuals from seven different ornithological collections: Cornell University, Harvard University, Louisiana State University Museum of Natural Sciences (LSUMZ), Western Foundation of Vertebrate Zoology (WFVZ), La Salle and Adolfo Pons Natural History Museum, Natural Science Institute from the National University of Colombia (hereafter ICN) and Alexander von Humboldt Institute (hereafter IAvH). In the last two ornithological collections I took the measurements whereas in the other collections the information was collected by the museum curator.

For each museum individual, age, sex and location were extracted from the identification cards, and the following lengths were measured: flattened wing, tail, tarsus, and bill (from the nostril to the tip) (Figure 1). At ICN and IAvH, I additionally measured the width and height of the bill and the reflectance on feathers from the crown, chest, wing, and tail. Finally, at IAvH, I collected a tissue sample from 15 individuals for standardization of the molecular sexing protocol, from which 5 individuals were of unknown sex. Samples were placed in Eppendorf tubes of 5 mL and stored at -30°C.

Phenotypic characterization of wild individuals

To characterize further the phenotypic differences between males and females I also collected morphological measures on wild individuals. For each captured individual, I measured weight, length of flattened wing, tail, tarsus, bill (from the nostril to the tip), and bill width and height (Figure 1).

I also collected, feathers from the crown, chest, wing, and tail to measure plumage coloration in the lab, and the tenth secondary feather of the two wings or a growing feather with blood-irrigated cannons for molecular sexing as indicated in Gratto-Trevor (2004). The feathers were stored at 8°C in fully identified paper envelopes.

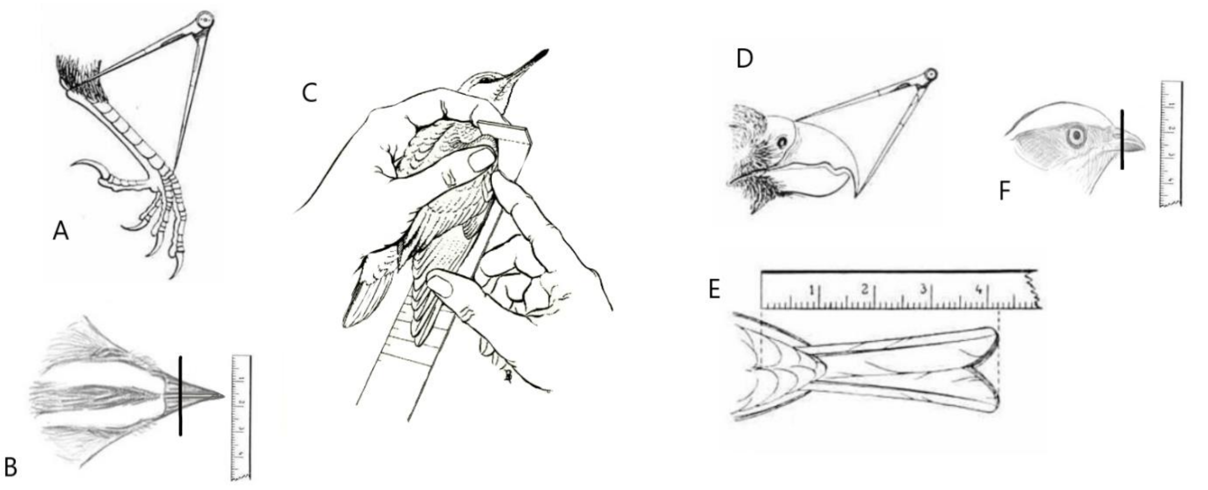

Figure 1. Measurement lengths of: A. tarsus, B. bill width, C. flattened wing, D. bill from nostril to the tip, E. tail and F. bill height are shown. Modified from: (Reichenow, 1913)

Color measurements

To characterize differences in plumage coloration, I measured reflectance on feathers from the crown, chest, wing, and tail. On museum individuals I took the measure on the individual, whereas on wild individuals I collected feathers and mounted them on a black cardboard. I used the Ocean Optics miniature flame spectrophotometer with a power source for halogen and deuterium lights (Ocean Optics Inc. DH-2000-BAL) and a bifurcated fiber optic cable to quantify color reflectance of all feathers (Figure 1c) across the UV and visible spectrum (189 nm – 1033 nm). I quantified the reflectance of feathers following a previously established protocol written by Bravo, G. A/ & Marcondes, R. S. (nd). I recalibrated the dark and white reflectance standard between each new feather measurement to minimize instrumental drift, using the OceanView software version 1.6.7 (Ocean Optics team, 2020).

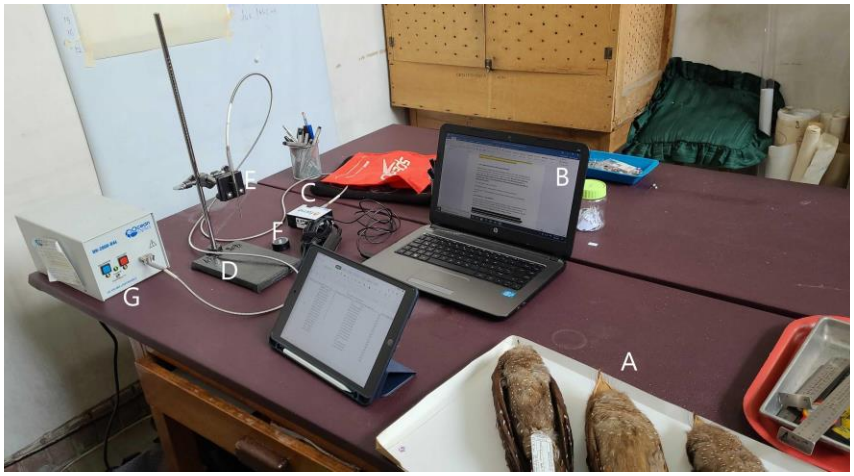

Figure 1c. Spectrophotometer assembly for data collection in the Ornithological collections. A. Museum specimens, B. computer with the OceanView software version 1.6.7, C. Ocean Optics miniature flame spectrophotometer, D. modified support, E. bifurcated fiber optic cable, F. white standard and G. power source for halogen and deuterium lights (Ocean Optics Inc. DH-2000-BAL)

Molecular sexing

To determine the sex of the wild and museum individuals of unknown sex I used a protocol based on the heterogametic variations of the sexes (ZW females and ZZ males; (Morinha et al., 2012)). First, I standardized the DNA extraction procedure using feathers of *Anas platyrhynchos domesticus* of known sex (Appendix 1). To do this, I modified as necessary, the protocol reported on the Qiagen blood and tissue instructive (Qiagen, 2020). Then, using the extracted DNA, I tested the performance of the primers 2550F/2718R, P2/P8 and 1237L/1272H. I selected the pair of primers that showed more clearly the differentiation between the bands in a 2.5% agarose gel.

With the standardized protocol, I proceeded to extract the DNA from feathers (wild individuals) or tissue (museum individuals). For the tissue, I modified some steps of the protocol (Appendix 2). Then, I amplified the extracted DNA under a PCR program consisting of an initial denaturation at 94°C for 5 minutes, 45 cycles of: 45s at 94°C, 45s at 46°C and 1 min with 30 seconds at 72°C. A final extension of 10 min at 72°C with an inactivity period at 12°C (until samples were removed). In the case of the feather and the tissue, the DNA samples were placed again under the same PCR program at 25 cycles. The fragments obtained from the PCR were visualized in a 2.5% agarose gel using DNA samples from individuals of known sex as control (i.e., male, and female *Anas platyrhynchos domesticus*) (Figure 2).

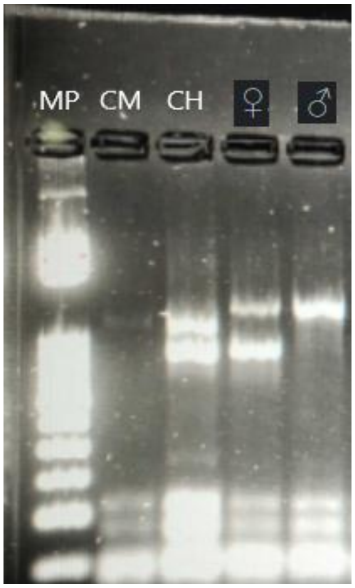

Figure 2. Sample of the visualization of a 2.5% agarose gel of the molecular sexing of *S. caripensis.* 50 bp marker weight (MP), control male DNA from *A. platyrhynchos domesticus* (CM), control female DNA from *A. platyrhynchos domesticus* (CH), samples from a wild female (♀) and a wild male (♂) of previously unknown sex.

Data analysis

Plumage coloration

I delimited the spectrophotometer wavelength values for visible and UV spectra using the package psych version 2.2.3 (Revelle, 2016) in R version 4.1.1 (R Core Team, 2020), and then I identified the peak value of the wavelength in the visible spectrum (380-780 nm) and in the UVC spectrum (100-279 nm). These values were then used to characterize color differences among males and females.

Quantification of sexual dimorphism

To determine the degree of allometry between the sexes I applied the Rensch rule (1950) using the package lmodel2 version 1.7-3 (Legendre, 1988) in R version 4.1.1 (R Core Team, 2020). I constructed a type II regression model using as a proxy of body size the length of the flattened wing measurements (log10 transformed) of females and males, on the X and Y axis, respectively. Then, I extracted the Ranged Major Axis (RMA) by permuting the model ninety-nine times to be fitted each time, to infer the mating systems. Under the Rensch's rule the RMA values equal or lower than -1 indicate larger males, values equal or larger than 1 represent larger females, and values larger than -1 or lower than 1 show that male and female do not have notorious variation in body size (Dale et al., 2007; Rensch, 1950).

Additionally, to assess the degree of sexual size dimorphism, I used the Storer's dimorphism index (SDI; Storer, 1966):

$$SDI = 100\left(\frac{(\underline{x}_a - \underline{x}_b)}{(0.5)(\underline{x}_a + \underline{x}_b)}\right) \qquad \textbf{(Equation 1)}$$

Where *x* represents the character evaluated, in this case the morphological traits that were obtained from museum and wild individuals, the subscripts *a* and *b* denote male and female. SDI values below 0 indicate that males are larger than females and above 0 that females are larger.

Phenotypic characterization of males and females

To quantify the differences between males and females I examined the morphological variation between sexes in four morphological measurements and two-color variables. I first used a PCA to reduce the dimensionality of the morphological measures. Then, I ran two Quadratic Discrimination Analysis (QDA), one for the morphological variables and the other for the color variables. To do this, I first randomly split the data in a train set containing 80% of the observations, and a test set which contained the remaining observations. In both models, sex was fitted as the response variable and length of bill, flattened wing, tail, and tarsus as the explanatory variables.

Both analyses were done in the MASS package version 7.3-55 (Venables & Ripley, s. f.) in R version 4.1.1 (R Core Team, 2020).

Results

I collected measurements on a total 99 museum specimens, of which 25 individuals did not have the description of the sex in the cards (this left me with 75 individuals for the analysis), and 16 wild individuals, which all of them were of unknown sex.

Molecular sexing

I sexed 11 of the 16 wild individuals using the primers 2550F/2718R associated with the CHD1 gene (Fridolfsson & Ellegren, 1999). I could not sex five individuals probably because I obtained low DNA concentrations (<10 ng/µl) which prevented a correct visualization of the bands in the gel (Figure 3). The samples of museum individuals had on average DNA concentrations of 40 ng/µl but could not be read in agarose gel or in the polyacrylamide gel (Figure 4). This may be because the DNA was fragmented due to the oldness and deterioration of the specimens (Sawyer et al., 2012).

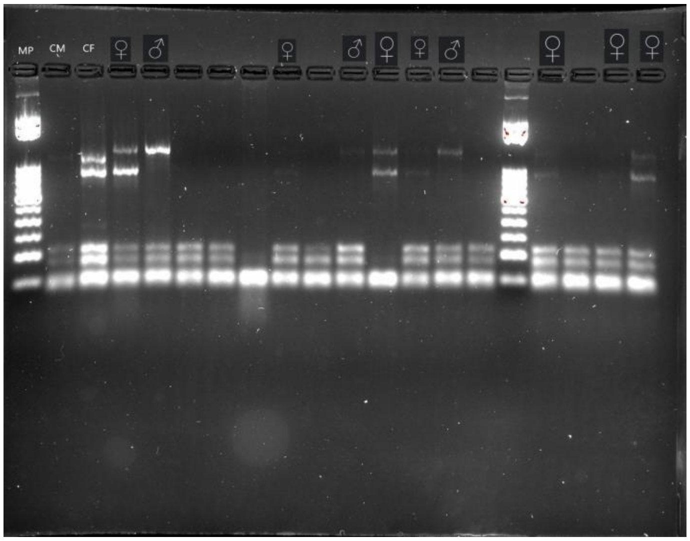

Figure 3. 2.5% agarose gel, showing the weight marker (MP), control male from *Anas platyrhynchos domesticus* (CM), control female from *Anas platyrhynchos domesticus* (CF) and different wild individuals are seen of *S. caripensis* sexed.

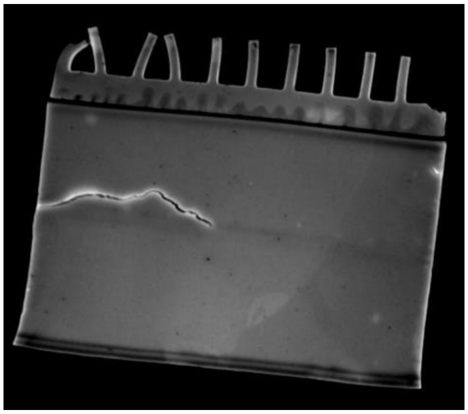

Figure 4. Polyacrylamide gel at 8%, where the individuals in the museum were sexed. This sexing was not possible with the techniques performed.

Quantification of sexual dimorphism

I obtained an RMA of -0.35 (CI= 2.5%) and an intercept of -8.1 (CI= 2.5%) (Figure 5), from the Rensch analysis which reveals that males and females do not differ among them in their morphology. Moreover, the RMA value indicates that *S. caripensis* has a monogamous mating system. Also, the Storer index yielded the following values for morphological traits: flattened wing SDI = 0.71, tail SDI = 0.68, tarsus SDI = 0.54, bill height SDI = -1.38, bill width SDI = -9.37 and bill length SDI = -4.87, indicating slight differences in the bill morphology between males and females.

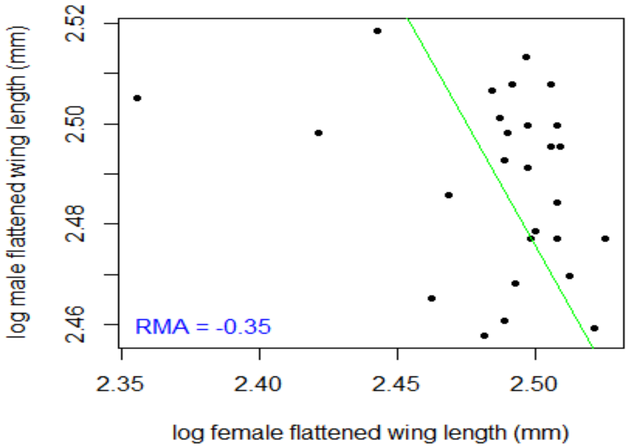

Figure 5. Type II linear regression showing the Ranged Major Axis (RMA) for *S. caripensis*, with a value of -0.35.

Morphological and color characterization

I collected morphological information on 75 museum individuals and 16 wild individuals, feather coloration in 33 museum individuals and 11 of wild individuals. In general, morphological and color traits do not seem to differ between males and females (Figure 6). However, the bill length shows a slight differentiation between sexes, with males exhibiting longer and wider bill.

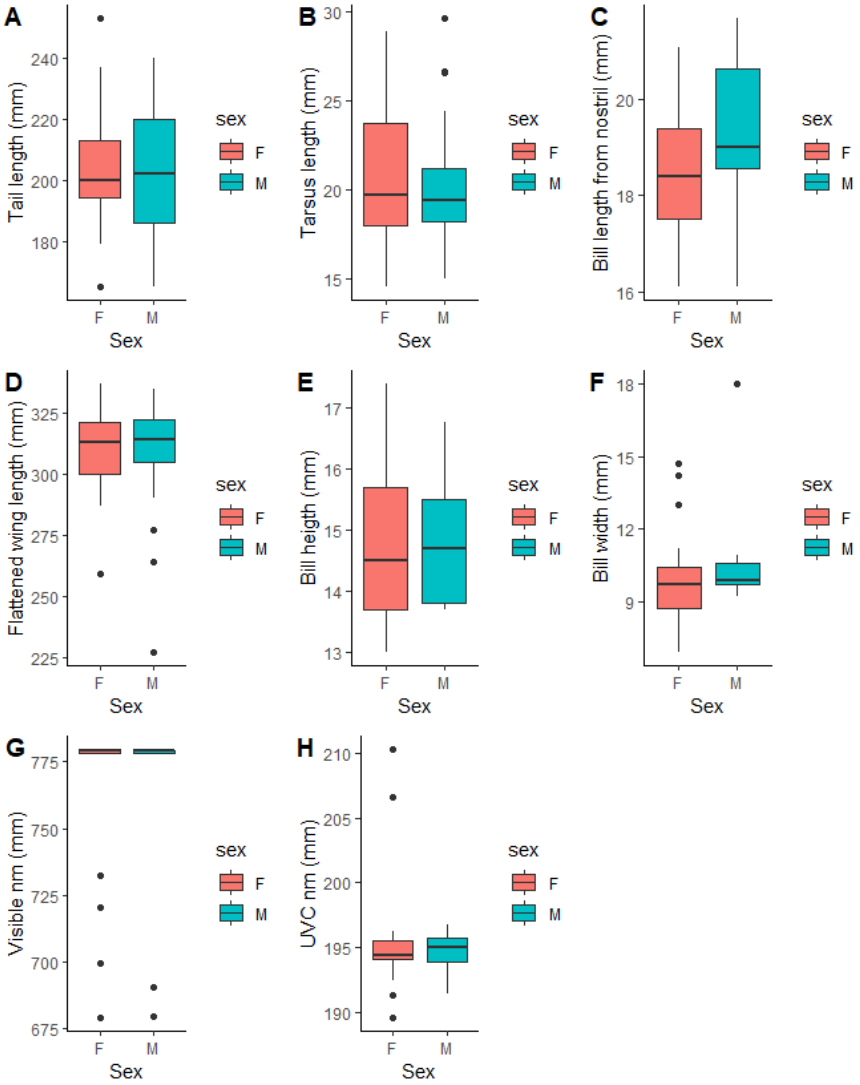

Figure 6. Boxplot representation from the morphological and color characters in the sexes of *S. caripensis*.

The first to dimensions of the PCA for morphological traits captured 70.9% (Figure 7). Dimension 1 captured 43.6%, with the largest contribution from the: tarsus, flattened wing, and tail. Dimension 2 captured 27.3% of the variation with only one variable contributing, the bill length. Because the measurements of the height and width bill had small weight contributions to the PCA I excluded them for the QDA analysis. The PCA for color traits in the dimension 1 captured 68.27% where just the UVC variable contributed, and the dimension 2 captured 31.7% where UVC and visible nm variables contributed equally.

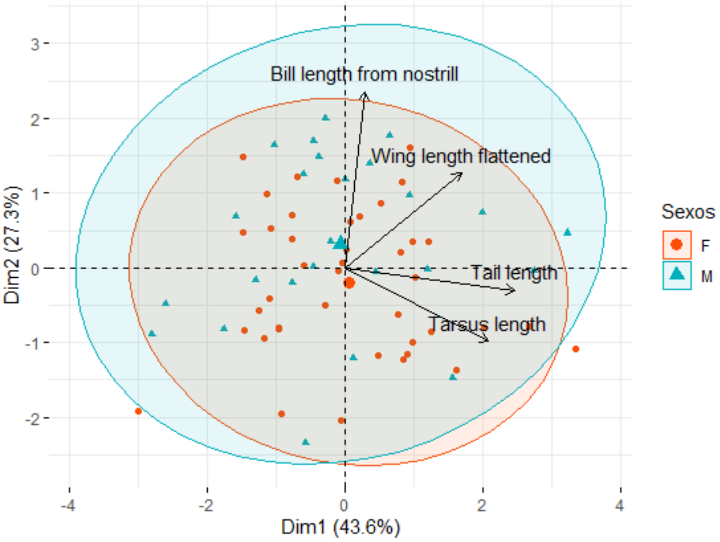

Figure 7. Principal Component analysis (PCA) of the sexes using morphological measurements of *S. caripensis*, obtained from museum and wild individuals.

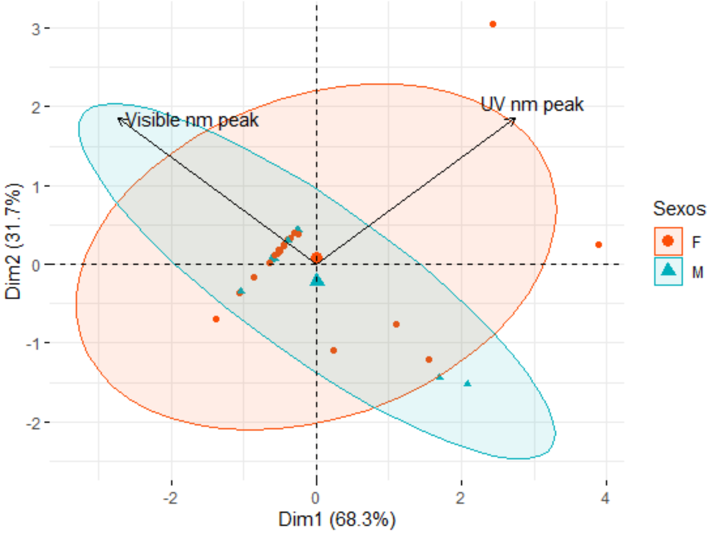

Figure 8. Principal Component analysis (PCA) of the sexes using color measurements of *S. caripensis*, obtained from museum and wild individuals.

The model accuracy of discriminant analysis (QDA) for morphometric traits is 0.53, whereas the QDA for plumage coloration is 1. Indicating that with morphological variables, it is not possible to differentiate between sexes, whereas color variables show a slight difference between males and females in the UVC spectrum.

Discussion

The characterization of the sexual dimorphism in species with slight phenotypic differences such as *S. caripensis* requires examining the variation of several phenotypic traits, and the use of molecular techniques to validate the results. Our results indicate that males and females of *S. caripensis* are similar in size, as previously reported by Snow (1961). However, examination of plumage color indicates that there may be sex related differences in coloration. Finally, the similarity in morphological measures between sexes suggests that *S. caripensis* exhibit a monogamous mating system.

Sex determination in species with subtle sexual dimorphism rely on the use of molecular techniques for accurately sexing individuals (Griffiths et al., 1998; Morinha et al., 2012). The protocol that I standardized allowed me to sex 11 of the 16 individuals collected in the field. The low success of the protocol may be because the DNA concentration of some samples was lower than 10 ng/µl. In this study, samples obtained from tail and wing feathers especially those that were growing (pin feathers) resulted in good DNA quantity compared to samples extracted from crown and chest feathers. This is because the DNA concentration extracted from feathers can vary with the quality and type of the feather. For example, feathers from the superior umbilicus (i.e., in the juncture of the calamus and the rachis) and those with a calamus diameter larger than 1.5 mm are better DNA sources (Vili et al., 2013). For museum samples, although DNA concentrations were greater than 30 ng/µl, the bands could not be visualized on 2.5% agarose gel or 8% polyacrylamide gel, which indicates that the DNA may be highly fragmented. The degradation and fragmentation of DNA is a process that varies according to several factors, including the species, the conservation of the individual, and the preparation of the specimen, among many other hidden traps that generate inconveniences when performing molecular sexing (Wandeler et al., 2007). Additionally, age and the handling history of the specimen can affect the quantity and quality of DNA (Zhang et al., 2021) however, this factor cannot be easily controlled.

Traits that determine sexes in species with subtle sexual dimorphism may not be noticeable to the human eye (Bergeron & Fuller, 2018). In oilbirds, morphological traits exhibited subtle variations between the sexes but not enough to discriminate accurately males from females. Sexes differed mostly in the width and the length of the bill, which is larger in males. Larger beaks may be related with differences in the ecological niche, it may allow males to feed on larger fruits, but this hypothesis needs to be further studied. Color-related traits, on the other hand, showed differences between the sexes that allowed sex differentiation. This difference suggests that the slight difference in color—i.e., males are grayer than the females (Hilty & Brown, 1986), may be important for discriminating individuals of opposite sex and that birds are interpreting the color differently. However, future studies evaluating the visual perception in this species are needed.

Species were males and females are of similar size are hypothesized to exhibit a monogamous mating system (Dale et al., 2007). Our results indicate that *S. caripensis* may be monogamous, thus providing support to what was previously proposed by Roca (1992) and Cleere & Nurney (1998). A monogamous mating system indicates that parental care may be shared among sexes, and suggests that individuals need to carefully select their mate choice to avoid the fitness cost of choosing a wrong partner (Dunn et al., 2001). In oilbirds, mate selection does not seem to be based on morphological traits since there is little variation between the sexes, which opens the question about the characters that allow choosing a good partner. Our results suggest that individuals may use color to retrieve information about potential mates. However, color is not an inherent property of the objects, but rather a construction of the brain when perceiving objects (Bennett et al., 1994). Thus, it becomes important to investigate how *S. caripensis* perceives their environment and their conspecifics.

My study indicates that *S. caripensis* have subtle differences in size between the sexes and suggests that it is a monogamous specie in addition that color may play an important role in the differentiation of the sexes, and possibly in mate choice. Moreover, feather coloration may be a candidate trait that allows non-invasive techniques for sex discrimination. However, understanding color traits and their ecological and evolutionary role needs the development of proper vision models, a topic that needs to be further studied and that will allow us to understand better conspecific discrimination. Finally, the DNA extraction technique developed in this study needs to be fine-tuned depending on the sample type, thus allowing us to use it for a wide range of samples.

Acknowledgments

A special acknowledgment to Dr. Adriana Maldonado Chaparro, who thanks to her support and dedication this project has been carried out with the highest standards. In the same way, thanks to Dr. Victoria Villegas, Dr Maria Agüero and Duvan Morales for their unconditional support and guidance in the laboratory.

To the Universidad del Rosario and the Max Planck Partner Group in Behavioral Ecology and Conservation, for their financial support. To the laboratory staff of the Universidad del Rosario, who were always with the best disposition.

To Dr. Gustavo Bravo and Gustavo Alarcon Nieto for their support and shared knowledge of birds.

To the different ornithological collections that were kind enough to share with me the morphological measures of the oilbirds: Cornell University, Harvard University, Louisiana State University Museum of Natural Sciences (LSUMZ), Western Foundation of Vertebrate Zoology

(WFVZ), La Salle and Adolfo Pons Natural History Museum, Facultad de Ciencias Naturales de la Universidad Nacional de Colombia, and Instituto Alexander von Humboldt.

Also, thanks to my colleagues Juan Mongui and Melissa Ardila, and my family for their support and collaboration.

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