



# Sexual dichromatism in a cryptic poison frog is correlated with female tadpole transport

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## Abstract

Sexual dichromatism has provided important information for understanding sexual selection, but its link to reproductive success has received little attention. Poison frogs and their relatives within the superfamily Dendrobatoidea present striking color variation. Despite this variability, evidence of sexual dichromatism in the over 330 species described is limited to the gular region of some cryptically colored species. *Colostethus imbricolus* is a cryptically colored dendrobatid with distinct orange and yellow spots at the axillar, inguinal and femoral regions. Here we show that these spots stand clearly out from the environment during behavioral displays and that they present marked sexual differences in their conspicuousness, with females having more conspicuous spots. Unlike most species of Dendrobatoidea that provide parental care in the form of male tadpole transport, we found that in *C. imbricolus*, females performed this behavior. By correlating color measurements and behavioral observations, we show that females with a higher number of transported tadpoles are also the most conspicuous. Our findings show a significant association between sexual dichromatism of the spots and female parental care while opening exciting perspectives for the occurrence of both traits. In addition, our results provide significant insights to address the function of dual-color patterns (i.e., cryptic from distance—aposematic from nearby) in amphibians.

**Keywords** Sexual dichromatism · Parental care · Tadpole transport · Dendrobatoidea · *Colostethus imbricolus*

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## Introduction

Sexual dichromatism, where males and females differ in coloration, has provided essential evidence for understanding sexual selection (Andersson 1994) and has been predominantly studied in birds (Dunn et al. 2015), fishes (Kodric-Brown 1998), and butterflies (Allen et al. 2011). In amphibians, it has been described in Bufonidae, Hylidae, Hyperoliidae, Ranidae, and Dendrobatoidea (Grant et al. 2006; Bell and Zamudio 2012; Bell et al. 2017; Rojas 2017; Portik et al. 2019), but unfortunately, the functional implications are mostly unknown.

Several species of neotropical poison frogs from the superfamily Dendrobatoidea, which includes the sister clades Aromobatidae and Dendrobatidae, are well-known for the presence of aposematic coloration and recognizable coloration patterns (Silverstone 1975a, 1976; Myers and Daly 1976; Grant et al. 2006, 2017; Brown et al. 2011; Rojas 2017). Yet, cryptic coloration is also a common feature of different genera in both families (Grant et al. 2006, 2017; Rojas 2017). Sexual dichromatism in Dendrobatoidea is relatively common in cryptically colored species within Aromobatidae, but is absent or inconspicuous in most aposematic species (Bell et al. 2017; Grant et al. 2017; Greener et al. 2020). However, most reports are limited to dichromatism of the gular region, whereas sexual dichromatism in other body regions is very rare (Engelbrecht-Wiggans and Tumulty 2019). Although it is assumed they mediate visual communication, the functional relevance is unknown.

Dendrobatid frogs are also well-known for their complex parental care behaviors, including egg attendance, trophic-egg feeding of tadpoles, and tadpole transport, with the latter occurring in several species (Lötters et al. 2007; Summers and Tumulty 2014). Typically, tadpoles are transported on the dorsum of the parents to water phytotelmata or ground-level water bodies such as pools or small streams to complete metamorphosis (Crump 1996; Lötters et al. 2007; Kahn et al. 2016). In most species, tadpole transport is carried out predominantly by the males, but eventually, females could be involved in tadpole transport when males abandon their parental task (Zimmermann and Zimmermann 1980, 1981; Caldwell 2005; Grant et al. 2006; Ringler et al. 2013). In addition, predominant maternal tadpole transport is considered a synapomorphy of the *Colostethus latinasus* Group and the genus *Oophaga* and has also been reported in very few species of *Allobates*, *Hyloxalus*, and *Mannophryne* (Grant et al. 2017; Carvajal-Castro et al. 2021). However, reports of the predominant role of females in tadpole transport may be based on isolated observations and are not seldomly accompanied by descriptions of male tadpole transport (La Marca 1994; Grant 2004; Grant et al. 2006; Acosta-Galvis and Vargas-Ramírez 2018; Carvajal-Castro et al. 2021) or are contradictory (Grant 2004; Grant et al. 2006). In addition, behavioral observations showed that males of different *Oophaga* species also transport the tadpoles (Weygoldt 1980; Cossio 2008; Killius and Dugas 2014; Palacios-Rodriguez, pers. obs). Thus, till present, the only well-documented cases in nature in which tadpoles are transported by females and not by males in Dendrobatoidea have been described in *C. panamansis* and *C. pratti* (Wells 1980, 2010). Regardless of the sex that conducts this behavior or whether it is predominant or facultative, tadpole transport in dendrobatids has not been correlated with any signaling component in coloration or body condition.

*Colostethus imbricolus* is nested within the *C. latinasus* Group also including *C. inguinalis*, *C. latinasus*, *C. pratti*, and *C. panamansis* (Grant et al. 2017), and represents a unique opportunity to evaluate color-driven questions in poison frogs because: (a) it belongs to the Dendrobatoidea clade where tadpole transport is predominantly conducted by females, and (b) as other members of the genus, it has marked orange spots at the level

of the axillary, femoral and inguinal regions contrasting the brownish color of dorsal skin (Silverstone 1975b). Here, we first conducted field behavioral observations to understand the circumstances in which the colorful spots from *C. imbricolus* are visible in nature, and evaluated variation among the sexes in body condition. Based on these data, we hypothesize that color variability in females' groin spots is correlated with their body condition and reproductive status discriminated as carrier vs. non-carrier of tadpoles. We further tested this hypothesis by measuring the conspicuousness of the spots and by examining whether they are correlated with the number of tadpoles transported.

## Material and methods

### Study system

*Colostethus imbricolus* is distributed in the Pacific lowlands of Chocó, Colombia, and is strongly associated with ravines and riparian forests (Silverstone 1975b). This research was conducted in a lowland forest in the locality of Victoria (05°30'N 76° 52'W) between March 2019 and April 2020.

### Sexual recognition and behavioral observations

Males were distinguished from females based on whether they were vocalizing and on the presence of dark vocal sacs. Behavioral observations on sexual interactions and tadpoles transport were registered between 05.00 to 18.00 h using focal animal, sequence, and all occurrence methods (Martin 1986). The reproductive status of females was differentiated among those that were carrying tadpoles (carriers) on their dorsum, and those that were not (non-carriers). Given that all tadpoles transported by each female (range 21–28; mean  $25 \pm 2.2$ ) were observed descending from the female's dorsum in a single event ( $n=8$ ), the number of tadpoles transported can be considered a stable character for each carrier specimen. To minimize the risk of misidentifying the condition of non-carriers as happenstance related to the specific time of the observation, these females were observed throughout the day for three consecutive days. Though it might not be discarded that a non-carrier female had recently conducted transportation, whether this was the case, the inclusion of a female within this category is a conservative criterion that will not affect true color differences between both females' categories. All specimens were collected by hand and kept in a moistened plastic container until fieldwork was finished. Photographs were taken from each specimen, and those from the dorsum were used to count the number of tadpoles. All observations were made by the same researcher and were discussed routinely with all co-authors.

### Measurements of body color and body condition

Color reflectance of each specimen was calculated from four measurements of the light reflectance on color spots, including at least one measurement from axillar, femoral, and inguinal regions and two measurements from dark dorsal regions. Reflectance measurements were taken in the field from representatives of the three categories: males ( $n=19$ ), carrier females ( $n=14$ ), and non-carrier females ( $n=8$ ), and from the substrate

(leaves, stones, logs) where each individual was found. All reflectance measurements ( $\lambda=300-700$  nm) were taken with a 600  $\mu\text{m}$  bifurcated fiber-optic (QR600-7-UV/VIS) coupled to a spectrometer (USB4000) using a pulsed xenon light lamp (PX-2) as a light source. Before each measurement, the lamp was calibrated with a white standard (WS-1-SL), and a probe with a rubber back cover was used to exclude ambient light. All equipment and the software were obtained from Ocean Optics Inc. (Dunedin, FL, USA). Measurements were taken at a distance of 2 mm and perpendicular ( $90^\circ$ ) to the surface. These data were used to generate reflectance curves for each specimen, expressing reflectance percentage and wavelength as dependent and independent variables, respectively. To determine reflectance differences within each group, 95% confidence intervals were calculated. Conspicuousness was estimated by comparing reflectance measurements of the color spots against the background reflectance under an independent vision system of potential receptors (Endler 1990). This method allows adopting the concept of color distance in a neutral color space, extending the results' interpretability to a visual system in which receptor properties are unknown (Endler 1990). These analyses were implemented in the R package Pavo that allows processing data obtained from different color metrics (Maia et al. 2013, 2019). Pavo was run in the R 3.6.0, run within Rstudio (RStudio Team 2020).

Two measurements were taken to characterize the body condition, size using the snout-urostyle length measured with a digital caliper (0.01 mm error) and weight calculated with a digital scale (0.1 mg error).

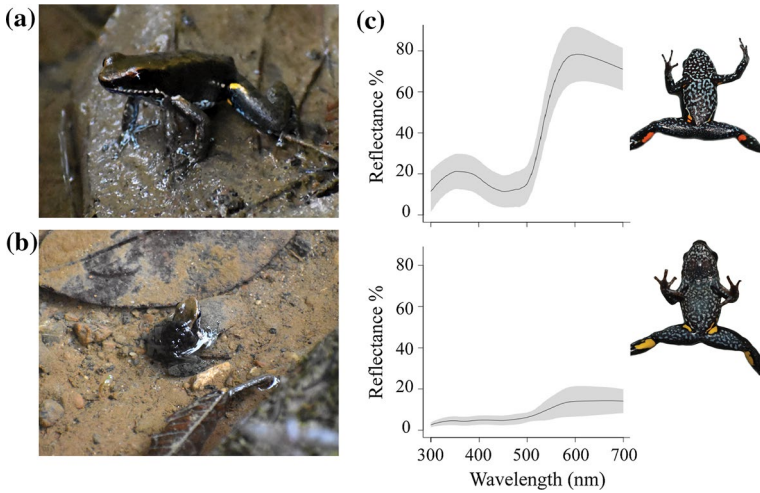
## Statistical analysis

The body condition index was obtained using a linear model of length and weight, and the residuals were used as the body condition index (BCI). Conspicuousness was used as a dependent variable throughout our Linear Mixed Model. First, the effects of the sex and the reproductive status of females and the BCI were tested on conspicuousness. Second, conspicuousness was correlated with the number of transported tadpoles. All statistical analyses were performed with the R 3.6.0, run within Rstudio (RStudio Team 2020).

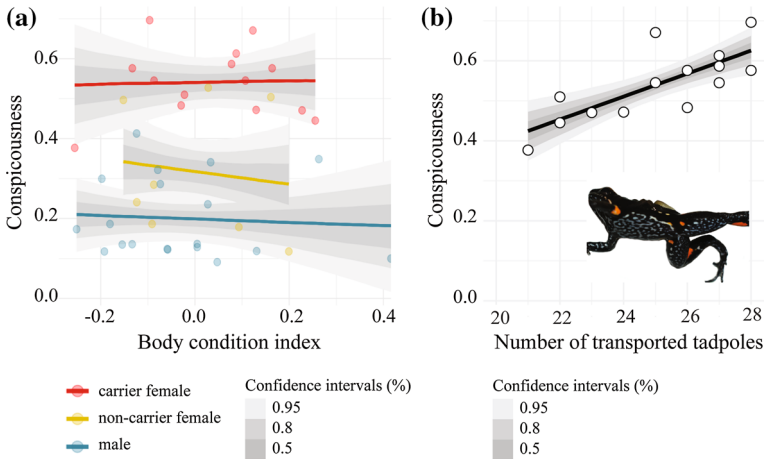
## Results

The yellowish and orangish spots from the hindlimbs and the axillar region of the forelimbs stood out during sexual interactions. These interactions ( $n=4$ ) can be summarized as follows: the male vocalizes in small rock crevices, and the female approaches and initiates a series of movements around the male that consists of raising its body either through the hindlimbs, forelimbs, or both (Fig. 1a). We did not observe any female-female interactions. Parental care in the form of tadpole transport was exclusively conducted by females. It consisted of transporting the tadpoles on the dorsum to a water pond within the stream, where they all descend one by one from near the female's vent. The number of tadpoles transported by each female ranged between 21 and 28 ( $25 \pm 2.2$ ,  $n=8$ ; Fig. 1b). Although females were not observed to raise the body during tadpole transport, the colorful spots were also visible while they were moving along the stream ( $n=8$ ).

Reflectance spectra showed marked sexual differences between adult males and females in the hindlimb and forelimb color spots (Fig. 1c). The conspicuousness of these spots was not explained by the effect of body condition (LMM:  $F=2.75$ ,  $P>0.07$ ; Fig. 2a), but instead, it was explained by the sex and the reproductive status (carrier vs. non-carrier



**Fig. 1** Behavior and sexual dichromatism in *Colostethus imbricolus*. **a** A female performing behavioral displays nearby a male. The colorful spots are noticeable during sexual interactions. **b** A female transporting the tadpoles on the dorsum. **c** Reflectance spectra of females (top) and males (bottom) were obtained from colorful spots occurring in axillar, inguinal and femoral regions. Gray shadows represent a 95% confidence interval



**Fig. 2** Correlation between conspicuousness, sex, and reproductive status in females from *Colostethus imbricolus*. **a** Correlation between body condition index and conspicuousness is linked to the sex and the reproductive status of females (tadpole carrier or non-carrier). Colour lines depict the measure of central tendency. **b** Positive correlation between the number of tadpoles carried by each female (white circles) and their respective conspicuousness value. The black line depicts the measure of central tendency. In both figures, the gray scaling denotes 95, 80, and 50% confidence intervals

females) of the specimen (LMM:  $F=20.91$ ,  $P<0.001$ ; Fig. 2a). Overall, females were more conspicuous than males, and within females, those that were carrying tadpoles on their dorsum were more conspicuous than those that were not. Within carrier females,

the number of transported tadpoles showed a positive correlation with conspicuousness ( $R^2=0.58$ ,  $P<0.0015$ ; Fig. 2b), but showed no correlation with the body condition ( $R^2=0.08$ ,  $P=0.31$ ).

## Discussion

Our field behavioral observations are consistent with the hypothesis that female tadpole transport is a synapomorphy of the *Colostethus latinasus* Group (Grant et al. 2017). Because male tadpole transport is the ancestral condition and the most frequent behavior found in Dendrobatoidea (Grant et al. 2017), the situation in this group represents a derived and rare trait. Female tadpole transport was well-documented in *C. panamansis*, where females also showed aggressive behaviors while defending their territories (Wells 1980). In contrast, our findings indicate that in *C. imbricolus* the body lifting behavior of females is instead used during courtship. This situation poses a challenge in understanding the establishment of mating system and parental care in *Colostethus*, because it represents an opposite scenario for the most traditional male's tadpole transport described in dendrobatids (Pröhl 2005; Grant et al. 2006; Wells 2010), and also because of the marked differences in the mating behavior within this group.

The functional implications of sexual dichromatism in *C. imbricolus* can be interpreted both in terms of visual communication and antipredator mechanisms, suggesting a potential interaction between sexual and natural selection, respectively. In the first case, we hypothesize that males may assess the conspicuousness of females during courtship. Although it seems counterintuitive thinking in males as the choosy sex, it was shown that females compete for their mates in *Alytes muletensis* (Bush and Bell 1997) and that males may select their partners in *Bufo andrewsi* (Liao and Lu 2009a, b) and some species of fishes (Rosenqvist 1990; Amundsen and Forsgren 2001). In the second case, the higher conspicuousness of females may represent an aposematic signal towards visual predators, which could decrease predation risk due to their high dislocations during tadpole transport. Both scenarios are discussed in detail in the following paragraphs.

Within amphibians, species in which females have more conspicuous body regions or are brighter than males have been only recently described in *Anomaloglossus beebei* (Engelbrecht-Wiggans and Tumulty 2019), and in some species of *Mannophryne* (Greener et al. 2020), both clades considered cryptically colored within Aromobatidae, and in some species from the distantly related Hyperoliidae (Portik et al. 2019). In contrast, the condition of more conspicuous males with drab females seems to be more widespread in anurans (Bell and Zamudio 2012; Bell et al. 2017), and in Dendrobatoidea was reported only in *Oophaga pumilio* (Maan and Cummings 2009). Based on published information (Bell et al. 2017; Portik et al. 2019) and our results, we can generalize that these differences could be related to the breeding system. In this sense, more conspicuous females would occur primarily, but not exclusively, in prolonged breeders and more conspicuous males occurring mostly in explosive breeders (Sztatecsny et al. 2012). Within prolonged breeders, dichromatism could be associated with higher predation risk related to high dislocations either to access mates (Portik et al. 2019), particularly in dendrobatids with the role of females in transporting tadpoles (this study).

Previous studies showed that in *O. pumilio* more colorful males win more fights and defend larger territories (Galeano and Harms 2016), but females may also defend small territories with adequate food resources (Meuche et al. 2011). In addition, the most toxic and

colored individuals produce fewer offspring (Dugas and Richards-Zawacki 2015). In contrast to this situation, females of *C. imbricolus* are not territorial, and those with the most colorful spots are the ones that carry the highest number of tadpoles. This positive correlation and the behavior of females in *C. imbricolus* is intriguing in terms of their functional significance and adaptive value. By conducting chemical analyses and further behavioral analyses, future studies could address many questions, including the toxicity, a dual-color pattern role (see Discussion below), and the potential existence of male mate choice in species of the *C. latinasus* Group.

Our results indicate that the conspicuousness, but not the body condition, is a good proxy of the reproductive fitness of females since specimens with more conspicuous spots carried the most tadpoles regardless of their size and weight. Similarly, no correlation was found between body condition and the number of transported tadpoles in males of *Ameerega trivittata* (Luiz et al. 2015) and the sexual dichromatic *Mannophryne trinitatis* (Downie et al. 2005), suggesting that both traits should be cautiously related while describing tadpole transportation in dendrobatids. Though our findings show that body condition does not explain the color variation among females, we cannot discard the possibility that spot coloration is related to the age of the specimens. In this scenario, although age and size are positively correlated in anurans (Duellman and Trueb 1986), this correlation may not be precise and would deserve further analysis. Besides the sexual differences described in our study, males and females in the genus *Colostethus* may exhibit differences in the color pattern of the gular region as it has been described in museum specimens of *C. panamansis* and *C. pratti* (Grant 2004). These differences, along with our results and our observations of dark vocal sacs in males of *C. imbricolus*, suggest that the mating system in species of the *C. latinasus* Group would involve visual signals from both males and females.

What mechanism generates the difference in coloration between males and females of *C. imbricolus*? Unfortunately, state-of-the-art art is very limited to answer this question conclusively, mainly because we yet do not have information on the structure and organization of the chromatophores and the pigments. However, we can speculate that different factors may be involved, including structural variables such as iridophores platelet thickness (Twomey et al. 2020b), chemical differences such as carotenoid composition (Twomey et al. 2020a), and the migration of melanosomes (Bagnara et al. 1968). For example, in the latter case, color changes in the females may be mediated by hormones (Sage 1970; Brown 1976), which could operate soon before the initiation of courtship. Supporting this hypothesis, color changes are under hormonal control in different animal species (Aspengren et al. 2009), and in amphibians, it was shown that various hormones like an  $\alpha$ -melanophore-stimulating hormone, epinephrine, and prolactin could induce color changes with variable levels of effectiveness (Brown 1976; Camargo et al. 1999; Kindermann et al. 2014). Interestingly, prolactin has known roles in parental behavior (Angelier et al. 2016) and thus could influence color changes in *C. imbricolus* females and prompt future maternal care behavior. If the hypothesis that females may change color during mating is true, this may represent a rare case of dynamic sexual dichromatism in anuran females.

Finally, *Colostethus imbricolus* was traditionally defined as cryptic but has indeed a dual-color pattern that might have two distinct functions; crypsis, which would serve to avoid predators from a distance, and conspicuous spots, which would act as an aposematic signal at shorter distances. This inference is supported by a previous study in the aposematic *Dendrobates tinctorius* (Barnett et al. 2018), but also by studies in insects and mammals (Tullberg et al. 2005; Caro et al. 2013; Ruxton et al. 2019). It seems evident that the dorsal brownish coloration matches the brownish environment of the leaves found in the stream, whereas to function as an aposematic signal, the colorful spots should be

linked to a toxic or noxious substance. Although in this sense, no study has yet analyzed the chemical profile of the skin of *C. imbricolus*, our preliminary assays with the extracts of *C. imbricolus* showed that they produce strong muscular contractions in *Mus musculus* (Palacios-Rodríguez et al. in prep). In addition, two other *Colostethus* species, *C. panamansis* and *C. ucumari*, possess toxic secretion rich in tetrodotoxin (Daly et al. 1994; Grant 2007). We are aware that the adaptive value of the colorful spots in *C. imbricolus* and other Dendrobatoidea needs to be experimentally tested. Still, our findings suggest that sexual selection and antipredator strategies should be considered while addressing the function of color patterns in amphibians.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s10682-021-10147-4>.

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**Author's contribution** P.P.-R. and M.G.-S. designed the research and conducted the fieldwork. P.P.-R., A.M., and A.E.B. analyzed the data. P.P.R. and A.E.B. wrote the paper. All authors reviewed the manuscript and approved the final version.

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## Declarations

**Conflict of interest** The authors have declared that no competing interests exist.

**Ethical approval** All procedures performed in this study were in accordance with the ethical standards of Comité Institucional para el Cuidado y Uso de Animales de Laboratorio (CICUAL) at Universidad de Los Andes. Procedures for capture, handling, and samples collections of live animals in the field were approved by Autoridad Nacional de licencias Ambientales (ANLA) (Permiso Marco de investigación No. 1177-Oct 9th, 2014).

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