Unveiling the polychromatism of Atelopus hoogmoedi (Anura, Bufonidae): Insights into adaptive significance and evolutionary implications

PATRICK SANCHES[1], Samuel Gomides[2], Youszef Bitar[3], Huann Vasconcelos[4], and Carlos Costa-Campos[4]

[1]Universidade Federal do Amapá
[2]Universidade Federal do Oeste do Pará
[3]Universidade Federal do Pará
[4]Universidade Federal do Amapa

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Abstract

Aposematic coloration plays an important role for species, as it serves as a clear signal of danger to visually-oriented predators regarding the potential toxicity of individuals displaying this condition. However, considerable gaps remain on this subject, and, primarily, empirical data are lacking to support robust discussions on the topic. The harlequin frog Atelopus hoogmoedi exhibits a range of aposematic colors across different populations, yet we still do not know how this characteristic was selected throughout evolution nor what the impacts of this characteristic are on the species' biology, ecology, and behavior. Considering that this topic deserves further in-depth studies, particularly due to being one of the most threatened groups of vertebrates and still lacking research, we present possible insights to guide future investigations on this subject.

INTRODUCTION

The high species diversity of anurans on the planet is a result of multiple evolutionary processes (Pyron & Wiens, 2013). However, we still lack robust information on how specific traits have emerged and which evolutionary forces have shaped them, such as behaviors and coloration patterns. The role of amphibian coloration remains poorly understood, considering the extensive array of colors and patterning with widespread polymorphism (Toledo & Haddad, 2009). The occurrence of multiple color morphs within a single species has intrigued researchers, leading to the exploration of various mechanisms underlying this polymorphism. Such mechanisms may be explained by genetic drift, natural selection, sexual selection, or a combination of these factors (Tazzyman & Iwasa, 2010; Rojas et al., 2015; Rojas et al., 2020).

Species coloration can play an important role to camouflage, solar radiation protection, thermoregulation and aposematism (Duellman & Trueb, 1986; Wells, 2007; Toledo & Haddad, 2009). Aposematism is a defensive strategy strongly linked to color polymorphism in poison anurans, in which colors function as signals to visually oriented predators, such as birds, to convey a clear message regarding unpalatability or the presence of toxic substances (Rojas et al., 2015). Additionally, for certain species, color patterns are useful for communicating about individual's health status or even physical fitness (Zamora-Camacho & Comas, 2019).

Intraspecific color variation in amphibians has been documented in several species (Richards-Zawacki et al., 2013; Gehara et al., 2013; Amézquita et al., 2017), providing an excellent opportunity to investigate the evolutionary mechanisms that drive the selection and fixation of such variability in certain populations across a species' geographic range. Cryptic coloration with dull colors is widely observed within the Bufonidae family and is likely the ancestral condition of this lineage (Loeffler-Henry et al., 2023). However, the emergence of species with conspicuous and vibrant coloration throughout the body or in specific parts has occurred in certain species, such as the genera*Atelopus* and *Melanophryniscus* (Baldo et al., 2012). Typically, these aposematic color patterns are associated with defensive mechanisms against predators and a warning for the presence of toxic alkaloids and tetrodotoxins of exogenous origin (Rueda Almonacid et al., 2005; Daly et al., 2008; Yotsu-Yamashita & Tateki, 2010; Mebs et al., 2018).

Toads of the genus *Atelopus* , distributed in the Neotropics, are well known for their bright coloration and large variation in color pattern, especially in populations from the Guiana Shield (Noonan & Gaucher, 2005; Lötters et al., 2022). Also, they are known to possess tetrodotoxin, which is an effective defense mechanism against predation (Mebs et al., 2018). Most species are restricted to the highlands of Andean zones while a few species alongside the Amazon River and Guiana Shield present wider distributions (La Marca et al., 2005; Lötters et al., 2011). The harlequin toad *Atelopus spumarius* sensu lato displays a *cis* -Andean distribution ranging from Ecuador and Peru, along the Amazon River, to the Guianas and the Brazilian states of Amapá and Pará. The species exhibit high color polymorphism along its distribution (Noonan & Gaucher, 2005). However, the *Atelopus spumarius* sensu lato encompasses at least two nominal species along its distribution, namely *A. hoogmoedi* , *A. manauensis* (Jorge et al., 2020b), and one candidate species in the south margin of the Amazon River (Silva et al., 2020). These populations have exhibited a complex and highly variable color pattern within and among populations.

The bufonid *Atelopus hoogmoedi* is a colorful small toad that until recently was known as *Atelopus spumarius* or *A. spumarius hoogmoedi* (Frost, 2022). The distribution of *A. spumarius* was supposed to range from the Andes to the Guianas, with a gap in between those two extremes in western Amazonia. Since the beginning of the century *A. spumarius hoogmoedi* was elevated to full species (Lötters et al., 2002, 2005). *Atelopus hoogmoedi* was described from French Guiana and is known to occur throughout the three Guianas and adjacent Brazil (Noonan & Gaucher, 2005).

In the Brazilian state of Pará the species was known from one small area in Monte Dourado and from a rather undefined locality "Brazil, 30 km S of the Suriname border" (material in RMNH), with outlying populations in Tucuruí, Serra de Carajás, Itaituba and near Santarém all four localities in Pará South of the Amazon River (Ávila-Pires et al., 2010). It was also recorded in the south margin of the Amazonas river in the Virola-Jatobá Sustainable Development Project (PDS) in the Xingu river basin which is a candidate species (Silva et al., 2020). The species is also known from several localities in Amapá (Lima, 2008; Silva-e-Silva & Costa-Campos, 2018) and from Uatumã river basin in Central Amazon (Jorge et al., 2020a). The typical color pattern of Brazilian populations mentioned are rather uniform in dorsal pattern (dark brown with vermiculate yellow to pale greenish lines on the back). On the other hand, individuals from different populations in Amazonia presented a great variation in color pattern with a significant differentiation from the typical pattern (Lötters et al., 2022).

MATERIAL AND METHODS

Data were obtained from field records of several expeditions to areas in Pará and Amapá state, Brazil (Table 1). Records were made in localities of *terra firme* rainforests within the Guiana Shield region, characterized by closed canopy and dense understory vegetation. One population was recorded in a native savanna forest (population I, table 1) in Amapá state. Another population (population L, table 1) in Pará state was recorded in a riparian forest with sandy and rocky soil bordering a stream drainage in a rainforest with vegetation that combines transition elements of Amazonian savannas. The dorsal color patterns of specimens (collected or not) were described using photographs. Although the description based on color photographs should be done with caution, the researchers made an in-field evaluation to assure that colors in photography do not appear distinct from the real. Each locality was georeferenced to produce a map showing the spatial distribution of color patterns. The color described is referred to the variation in color of the vermiculate dorsal pattern on the dark background. The maps showing the color pattern distribution were made using the software Quantum Gis version 3.24.1, all coordinates were projected as Datum WGS 84.

RESULTS

We found seven different coloration patterns of the vermiculate dorsal pattern of *A. hoogmoedi* , distributed throughout the species' range. We observed different coloration patterns in the same locality, but the predominant dorsal pattern in each population appears to be geographically structured. Colors of the vermiculate dorsal pattern on the dark background varied from yellow to orange-red, from white to pink, and from bluish-green to green. The yellow color morph is found in almost all populations with varying proportions (Figure 1). In Amapá, yellow individuals are mostly found in the west margin of Amapari river (populations A, C, and F; Figure 1) while bluish-green, green, and other colors can be found in higher proportions east of the Amapari river and (populations B, D, and E; Figure 1). Green and bluish-green are also very common patterns found in Amapá, especially in Serra do Navio region. The orange-red pattern is rare, being registered only in Tumucumaque (population B; Figure 1) and Colônia da Água Branca (population E; Figure 1). In Araguari river, white and pink are more common patterns (populations G and H; Figure 1). Pink is also a common pattern in Oriximiná, Pará state, with most individuals registered as having this color. However, in Pará state and in Jari, Amapá there are only a few individuals registered to capture all population variation (populations J, K, M; Figure 1). We observed more than a single color at a locality, with individuals exhibiting high variation in color and pattern, especially in Amapá. Lescure (1981) defined three morphs for*A. hoogmoedi* in the Guianas, with varying colors of dorsal pattern, but mostly based on the variation of the size of the sinuous dorsolateral longitudinal bands. We found the same variation in different populations of *A. hoogmoedi* in Brazil. Populations of Amapá exhibit thin dorsolateral bands (Figure 2a-f) similar to the morph "A" of Lescure (1981) from Attachi-Bacca, French Guiana. In Tapajós river, south Amazonas river, individuals exhibited color bands very variable in width with the predominance of color extending from the ventral surface the snout being more colored than black (Figure 2i), similar to the morph "B" of Lescure (1981) from Surinam. Specimens from Oriximiná, Pará has bands on the back that are wider than the black bands (Figure 2h and 2J) corresponding to the morph "C" of Lescure (1981). The population in Amapá savannas may be considered a new morph by having a predominantly yellow dorsal background with no dorsolateral bands but scattered black dots and stains (Figure 2g). In particular, the yellow pattern was the most widespread pattern and show a great variation with respect to the predominance of yellow bands on the dark background corresponding to the morphs previously defined (Lescure, 1981).

DISCUSSION

Polychromatism has been recorded in several anuran species and may serve distinct functions such as disruptive camouflage, aposematism, sexual identification, and others (Hoffman and Blouin 2000; Wells 2007). Although in the present study we observed multiple coloration patterns in individuals from the same locality, no studies have been conducted to assess the evolutionary mechanisms that have selected for these characteristics in the different populations of *A. hoogmoedi* . The diurnal activity displayed by species within this genus, coupled with their specific habitat in stream environments characterized by background noise, likely played a role in the evolution of visual communication signals (Heyer et al., 1990; Hödl & Amézquita, 2001).

Geographic isolation can generate phenotypic diversity in certain amphibian species (Rudh et al., 2007). However, this does not seem to be the case in *A. hoogmoedi* , as populations in close proximity exhibit distinct color patterns. Color variation among individuals in different populations has been described as a consequence of genetic drift associated with geographic features in *Adelphobates galactonotus* (Rojas et al., 2020). Furthermore, for some species dorsal coloration in males may play a role in female mate preferences (Maan & Cummings, 2008), although differences in coloration may not be sex-related for others (Ávila-Pires et al., 2010). The use of visual displays in *Atelopus* is described in the literature, both for the defense of territory and for aggression between individuals (Crump 1988, Lindquist and Hetherington 1996, 1998). Examining how the various color patterns of *A. hoogmoedi* may influence sexual selection or reproductive territory defense can provide insights into the selective pressures acting on this trait.

In certain polychromatic anuran species, color variation can lead to varying predation rates (Noonan & Comeault, 2009; Chouteau & Angers, 2011; Hegna et al., 2013; Amézquita et al., 2013; Willink et al., 2014). This can be attributed to the search image and prior predator experience exposed to different color patterns.

In terms of parsimony, it would be expected that a monomorphic color pattern within a species facilitates easier learning of the signal by predators (Rojas et al., 2015). This phenomenon is observed in Mullerian mimicry organisms (Chatelain et al., 2023). Polychromatism has been extensively studied in the context of predator-prey relationships, particularly when the models are geographically isolated, such as on islands (Hegna et al., 2013) or separated by rivers that act as a geographic barrier (Rojas et al., 2015; Jeckel et al., 2019). Populations exhibiting distinct color patterns that are geographically isolated may arise as a response to different predators in each locality. However, in the case of *A. hoogmoedi* which is distributed within a continuous forest landscape, the explanations may not be as straightforward.

Hence, the advantage of the polychromatic pattern in *Atelopus hoogmoedi* remains a mystery, prompting the need for further research encompassing genetic, behavioral, sexual and environmental selection. This characteristic provides an excellent opportunity to elucidate how evolutionary mechanisms such as selection, drift, or geographic isolation may operate to select for these patterns. Despite *A. hoogmoedi* being widely distributed in the Eastern Amazon and being one of the few species within the genus *Atelopus* that does not show strong evidence of population reduction (Valencia & Fonte, 2022), there are still significant gaps in our understanding of the species' biology and even its taxonomic delimitation (Silva et al., 2020).

We strongly encourage further investigations to elucidate the factors influencing color variation in this species. Scientific research on the biodiversity of the Amazon Rainforest has recently faced significant challenges due to funding cuts in the scientific budget implemented by the previous Brazilian government (Angelo, 2019; Fernandes et al., 2017; Escobar, 2019). Additionally, the increase in losses of natural areas in the last years (Peres et al., 2023) highlights the need to accelerate studies in the region before the loss of basic information. This jeopardizes the study and understanding of Neotropical biodiversity, particularly concerning a highly endangered group of vertebrates such as the anurans of the genus *Atelopus* . Therefore, it is imperative to allocate investments toward integrative research on the evolution and ecology of this genus of anurans.

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Tables

Table 1 Locality, number of individuals sampled (n) and basin of populations of *Atelopus hoogmoedi* in Amapá and Pará state, Brazil. We omitted the geographic coordinates of the localities for the safety of the populations.

Locality	Population	River	n	State
Tumucumaque	A	Amapari	3	Amapá
Tumucumaque	A	Amapari	3	Amapá
Tumucumaque	B	Amapari	3	Amapá
Tumucumaque	B	Amapari	2	Amapá
Cachaço	C	Amapari	5	Amapá

Locality	Population	River	n	State
Cachaço	C	Amapari	3	Amapá
Cachaço	C	Amapari	7	Amapá
Cachaço	C	Amapari	2	Amapá
Água Branca	D	Amapari	4	Amapá
Água Branca	D	Amapari	1	Amapá
Colônia	E	Amapari	9	Amapá
Colônia	E	Amapari	7	Amapá
Brilho de Fogo	F	Amapari	3	Amapá
FLONA AP	G	Araguari	3	Amapá
FLONA AP	G	Araguari	5	Amapá
FLONA AP	H	Araguari	1	Amapá
Ferreira Gomes	I	Araguari	2	Amapá
Jari	J	Jari	1	Amapá
Oriximiná	K	Cuminá	11	Pará
Monte Alegre	L	Curuá	3	Pará
Itaituba	M	Tapajós	1	Pará

Figure legends

Figure 1 Distribution map showing the distribution and proportions of color morphs of *Atelopus hoogmoedi* Amapá state and Pará state. Some letters indicate more than one point in a general area according to Table 1.

Figure 2 Color pattern variation in *A. hoogmoedi* from Amapá state (A–G) and Pará state (H) representing the yellow (A), bluish-green (B), Orange-red (C), white (D), pink (E), green (F), yellow background from savana (G), pink from Oriximiná, Pará state (H), yellow from Tapajós river and Oriximiná Pará.

Conflict of interest statement

There is no conflict of interest to declare

Author Contributions

Patrick R. Sanches: Conceptualization (lead); writing – original draft (lead); formal analysis (lead). Samuel C. Gomides: Supervision (equal); writing – review and editing (equal). Youszef O. C. Bitar: Conceptualization (supporting); Writing – original draft (supporting); Writing – review and editing (equal). Huann C. G. Vasconcelos: Writing – review and editing (equal). Carlos E. Costa-Campos: Conceptualization (supporting); Writing – original draft (supporting); Writing – review and editing (equal).

Data availability statement

The data that support the findings of this study are openly available at the Dryad Digital Repository: https://doi.org/10.5061/dryad.bzkh189fx

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ORCID

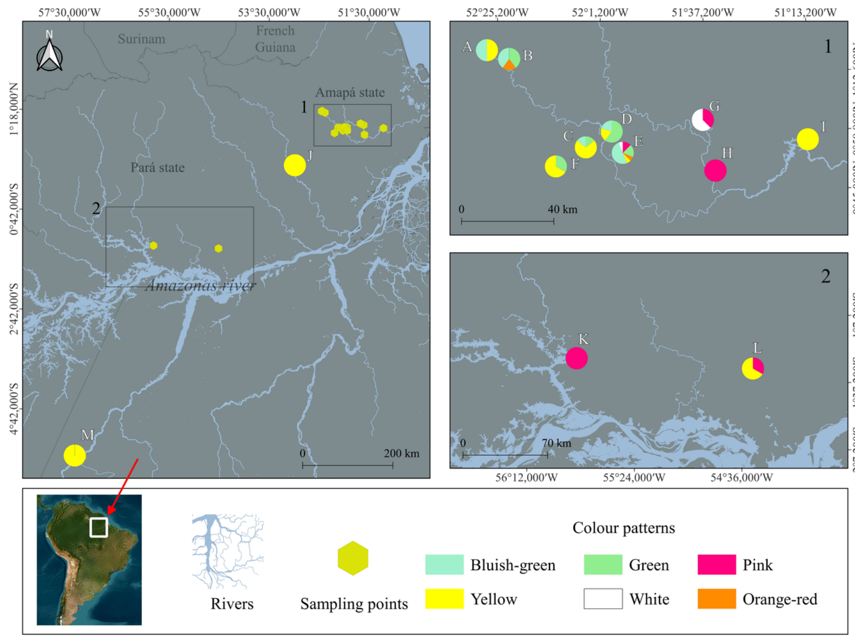
Patrick R. Sanches https://orcid.org/0000-0002-6346-3817

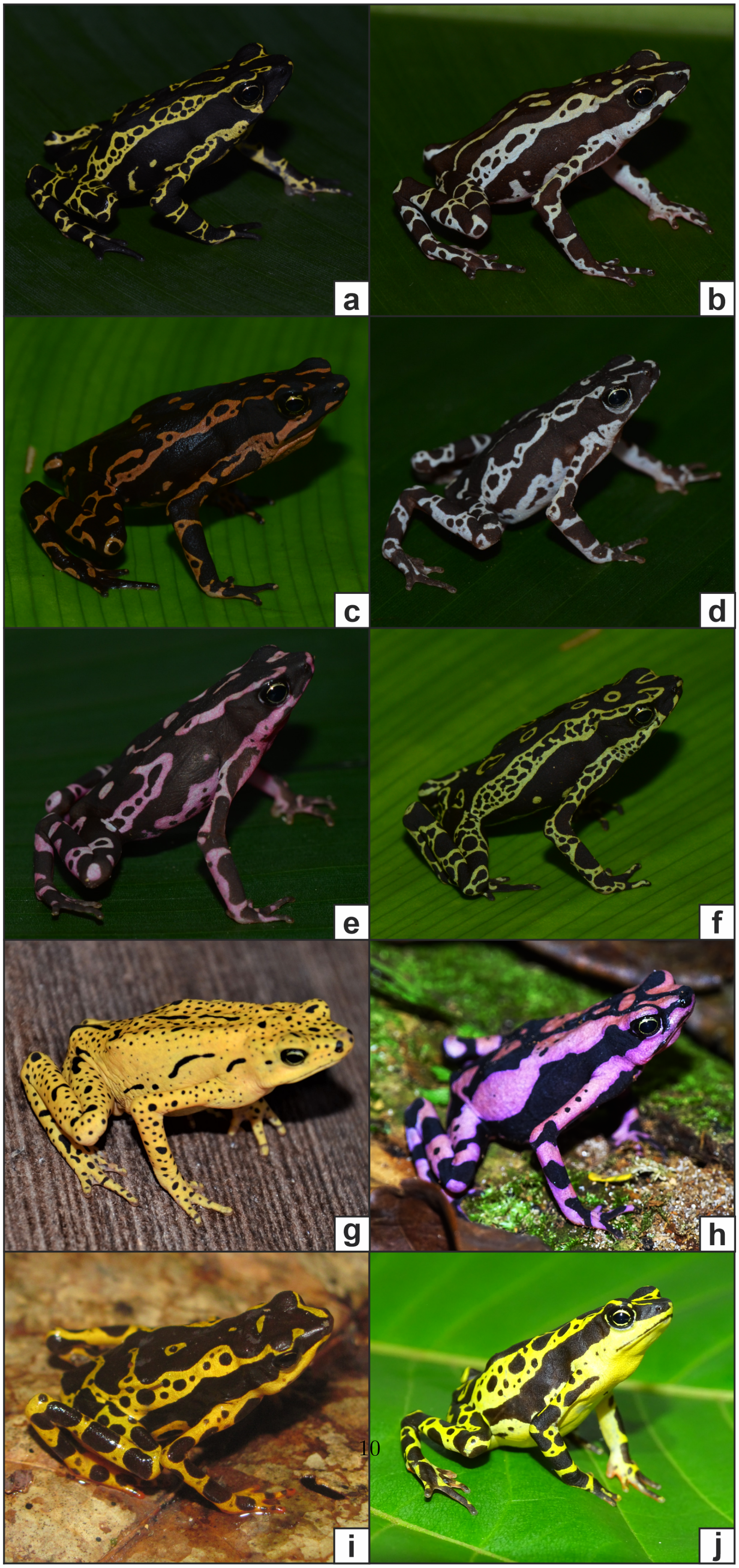
Samuel C. Gomides https://orcid.org/0000-0002-8454-5862

Youszef O. C. Bitar https://orcid.org/0000-0003-0074-4301

*Huann Carllo Gentil Vasconcelos*https://orcid.org/0000-0003-0911-0890

*Carlos E. Costa-Campos*https://orcid.org/0000-0001-5034-9268

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