

NATURAL HISTORY NOTE

Physiological Color Change in the Neotropical Tree Frog (*Pithecopus hypochondrialis*) as a Potential Mechanism of Nocturnal Camouflage

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Submitted October 12, 2023; Accepted May 7, 2025; Electronically published September 24, 2025

Online enhancements: supplemental PDF.

ABSTRACT: Animals employ various mechanisms for camouflage, including color change, that may facilitate habitat use. However, the extent to which these mechanisms operate under nocturnal conditions is unclear. To investigate this, we combined a background-induced color change experiment with visual modeling to test whether altering backgrounds for a tropical tree frog (*Pithecopus hypochondrialis*) could induce short-term color change under nocturnal conditions to match the viewing background, as perceived by three predator classes: snakes, mammals, and birds. We demonstrated that frogs can change color multiple times from green to brown and back across grass and leaf litter backgrounds in dim conditions. Frog visual contrast varied by predator and background. Brown frogs matched against leaf litter across all predators, whereas green frogs were more variable and comparatively less well matched against grass. Notably, frogs achieved near-optimal color matching against both backgrounds for avian predators, with green frogs matching into grass and brown frogs matching into leaf litter. Our study provides evidence that *P. hypochondrialis* undergoes rapid background-induced color changes at night maintaining effective camouflage, at least against avian predators. We emphasize the need to assess rapid color change against visually guided predators in natural conditions and the importance of understanding viewing conditions for illuminating the ecology and evolution of camouflage.

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Keywords: amphibians, coloration, crypsis, background matching, night, predators, prey.

Introduction

Coloration plays a fundamental role in the life history of animals, ranging from sexual selection, thermoregulation, and social differentiation to predator-prey interactions (Cuthill et al. 2017). Traditionally, color signals have been studied from a daytime perspective, considering various illuminations such as those found in shaded forest environments and open fields (San-Jose et al. 2019). It is generally assumed that many color displays evolve in concert with a diurnal lifestyle, as there is at least a million-fold increase in available light information in open daytime compared with nighttime conditions (Johnsen et al. 2006). Diurnal conditions allow for more efficient transmission of color-based information, increasing the likelihood of detecting visual stimuli across a diverse range of taxa. Indeed, nocturnal color vision itself was considered rare in nature because of sensitivity loss (Jacobs 1993). Recent evidence, however, suggests that color is an important dimension of visual perception for many taxa, including nocturnal animals, and it is more widespread than initially thought (Kelber and Roth 2006; Stöckl and Foster 2022).

Some nocturnal animals are capable of color and luminance perception under low illumination because of

morphological adaptations such as large eyes and pupils in combination with short focal lengths (Warrant 2004). Moonlight, being reflected sunlight, is the dominant source of nocturnal light in most terrestrial habitats. Its intensity, however, varies over time and across weather conditions and habitats (Johnsen et al. 2006), which shapes a suite of animal activities, including migratory orientation, hunting behavior, and antipredatory defenses (Foster et al. 2018). In terms of primary prey defenses, camouflage is considered the most commonly employed antipredatory strategy in nature (Stevens and Merilaita 2011; Merilaita et al. 2017), which involves several strategies that target the viewer visual systems to prevent recognition and detection. However, the mechanisms of camouflage among crepuscular and nocturnal species are far less studied compared with diurnal organisms (Cuthill 2019).

One of the many adaptations used by organisms to mediate visual camouflage is color change, which enables animals to effectively occupy different habitats (Duarte et al. 2017). Animals can undergo color change through morphological and physiological mechanisms. Morphological color change is characterized by the production, degradation, or chemical modification of pigments, which typically takes place over an extended period of time, such as during ontogeny (Figon and Casas 2018). In contrast, physiological mechanisms of color change are generally driven by specialized color-changing cells that modify light reflectance through intracellular pigment movement. These processes are often triggered by changes in external conditions such as the detection of predators or a change in abiotic conditions (Umbers et al. 2014). The timescale of these physiological mechanisms that drive color change is relatively brief, ranging from days (Choi and Jang 2014) to hours, minutes, or even seconds (Kindermann et al. 2014). However, the extent to which both long- and short-term color changes contribute to nocturnal camouflage in animals remains understudied.

While many amphibians are recognized for their color-changing abilities, and discussions about their ecological function have spanned nearly a century, there remain significant gaps in addressing the adaptive value of this phenomenon (Rudh et al. 2013). Kang et al. (2016) demonstrated that the tree frogs *Hyla japonica* are capable of changing color at night in response to both the color pattern and luminance of the substrate, which allows them to achieve camouflage and facilitates diurnal adjustments, thus reducing the physiological costs associated with this process. However, the mechanisms by which this color change may enhance camouflage against crepuscular and nocturnal predators in low-light conditions still need to be thoroughly investigated.

We recently observed a case of potential nocturnal camouflage through short-term physiological color change in

the Neotropical Hylidae tree frog species, *Pithecopus hypochondrialis*. We came across individual tree frogs that appeared to perfectly blend with a green leaf amid the grass, whereas others exhibited a brown coloration, visually blending with the leaf litter surrounding the palm swamp (figs. 1, S1; figs. S1–S3 are available online).

These nocturnal field observations prompted us to experimentally investigate whether *P. hypochondrialis* individuals could rapidly match their background colors in grass and leaf litter substrates, potentially resulting in short-term physiological color changes for nocturnal camouflage. Hence, we conducted a background-induced color change experiment to test whether altering the substrate affects the tree frog's coloration, resulting in camouflage through background color matching. We then quantified the degree of chromatic and achromatic matching against the background via models of the visual systems of one representative taxon from three important frog predator groups: a snake species, a mammal, and a bird species.

We tested whether the tree frogs adapt their coloration to minimize color contrast with the background they are exposed to according to the predator's visual system. We predicted (1) that green tree frogs will adopt a brown coloration if exposed to a leaf litter background to minimize visual contrast, (2) that they will adopt a green coloration when later exposed to a grass background, and (3) that if the tree frogs are repeatedly exposed to the same type of background (e.g., grass to grass or litter to litter), there will be no significant change in coloration or visual contrast.

Methods

Study Organism

The orange-legged leaf frog (*Pithecopus hypochondrialis*) is a widespread species found from South to Central America (Frost 2023). In Brazil it thrives in various ecoregions, ranging from very humid to arid areas with high temperatures, including the Amazon and the Cerrado savanna (Magalhães 2024). This nocturnal, arboreal species is observed from ground level up to 6 m high in shrubs and trees, where it rests on large leaves during the day and forages on arthropods at night (Alves Coêlho et al. 2021; Filho et al. 2022). These tree frogs prefer open habitats near the water, particularly around ponds, lakes, streams, and wetlands. In our study area, we observed them in grass, leaf litter, and small shrubs near palm swamps. Observations indicate that, despite having lipid glands and wiping behaviors to minimize water loss (Gomez et al. 2006), the species avoids sunny areas during the day to prevent dehydration and aid in camouflage. Specific surveys on the predators of this species are lacking; however, it is widely known



Figure 1: Schematic illustration based on our field observation, highlighting individuals of the species *Pithecopus hypochondrialis* displaying nocturnal color matching in response to their background (grass and leaf litter). Illustration by Felipe Capoccia.

that postmetamorphic anurans are preyed on by birds, mammals, and snakes (Toledo et al. 2007).

Field Captures and Background-Induced Color Change Experiment

We carried out active nocturnal captures of *P. hypochondrialis* individuals ($n = 9$) in palm swamps at Panga Ecological Reserve, Uberlândia, Minas Gerais, Brazil ($19^{\circ}11'40''\text{S}$, $48^{\circ}19'06''\text{W}$; figs. S1, S2). Captured tree frogs were individually placed in plastic bags and transported to a nearby field station (approximately 1 km away from the collection site). For the experiment, we used circular transparent arenas (27 cm diameter \times 20 cm height) with background substrates of grass or leaf litter collected from the same path where individuals were captured (figs. S1, S2). One day before the experiment, we used a subsample ($n = 3$) of the tree frogs to perform initial tests on the effect of daytime luminosity on color change by placing each individual tree frog into the arenas under natural daylight conditions (D65). After a period of 30 min in the arenas, however, no color changes were observed in individual tree frogs. Thus, after this first observation and considering that *P. hypochondrialis* is a nocturnal species, we acclimated all

experimental individuals to dark-room conditions before the onset of the experiment. We kept our experimental dark room at 24°C, matching the approximate natural local temperature. We collected individual data on initial reflectance (300–700 nm) before the experiment and after tree frogs were placed on each of the two experimental arenas with distinct background substrates (figs. 2, S2, S3). Our background-induced color change experiment consisted of randomizations of the initial substrate (leaf litter or grass) on which individual tree frogs were placed. Each frog was exposed to a distinct substrate background for a period of 25 min. After this period, we carefully removed individual frogs and recorded their spectral reflectance, as described above. Then, individuals were placed in arenas with the opposite background, with individuals ultimately being exposed to all possible combinations of background change in a random order (six measurements for each individual; see the supplemental PDF): for example, (1) grass \rightarrow leaf litter, (2) leaf litter \rightarrow grass, and their respective controls, (3) grass \rightarrow grass and (4) leaf litter \rightarrow leaf litter (figs. 2, S2, S3). As a control condition for each individual manipulation and measurement, we quantified the reflectance of frogs exposed for the same duration and under the same condition in a whiteboard-background control arena.

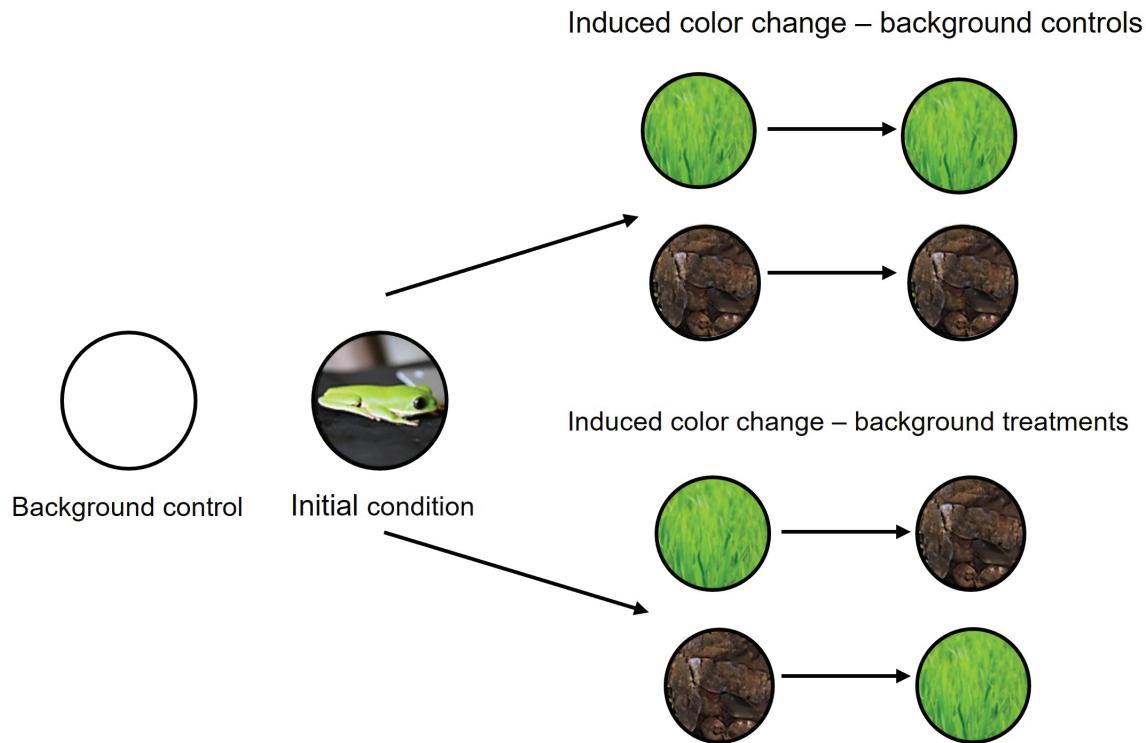


Figure 2: Flowchart depicting our experimental manipulations of background-induced color change in *Pithecopus hypochondrialis*. Each individual was exposed to all of the different control and treatment combinations.

Spectral Descriptors and Background-Induced Color Change

We used spectral measures of hue and saturation as explanatory variables in generalized linear mixed models (GLMMs) predicting experimentally induced changes in reflectance in our focal individual tree frogs. Following standard practice (Kemp et al. 2015), we defined the hue (or “color”) of each frog as the wavelength at which the peak reflectance was recorded. For saturation (or “richness”), we used an approach that divided the spectrum into four equal regions and calculated the relative reflectance within and across segments (see the supplemental PDF for further details; Montgomerie 2006). We then used hue and saturation as response variables in separate GLMMs with Gaussian distributions, with treatment as the sole predictor and frog identity as a random effect. We visually inspected residual distributions extracted from each GLMM to validate normality assumptions. We used emmeans (Lenth 2023) and stats packages in R (ver. 4.4.1; R Core Team 2024) for all statistical analyses.

Visual Modeling and Tree Frog Conspicuousness

To estimate the subjective conspicuousness of tree frogs against grass and leaf litter backgrounds to viewers, we used

the log-linear receptor-noise-limited model (Vorobyev and Osorio 1998; Vorobyev et al. 1998, 2001). For our representative snake predator, we selected the trichromatic garter snake (*Thamnophis sirtalis*), with cone peak absorbances at 360, 482, and 554 nm, and cone proportions of 1:1.6:7.3 (ratio of ultraviolet wavelength sensitive [UVWS] to medium-wavelength sensitive [MWS] to long-wavelength sensitive [LWS]; Sillman et al. 1997). For our mammal, we chose the dichromatic ferret (*Mustela putorius*), with cone peak absorbances at 430 nm (short-wavelength sensitive [SWS]) and 558 nm (LWS) in a proportion of 1:14 (Calderone and Jacobs 2003). For the avian system, we used the spectral sensitivity data of the tawny owl (*Strix aluco*), as reported by Höglund et al. (2019). Cone proportions for the owl model were set as 1:2:5 (SWS:MWS:LWS; Höglund et al. 2019). To address nighttime lighting conditions in visual models, we included the moonlight and starlight irradiance data from Johnsen et al. (2006). We set chromatic and achromatic Weber fractions to 0.02 and utilized all cones for calculating chromatic contrasts, while achromatic contrasts were estimated based on the long-wavelength cone (Siddiqi et al. 2004; Stuart-Fox et al. 2008; Maia and White 2018).

The receptor-noise-limited model allows for the estimation of noise-weighted chromatic (hue/saturation; ΔS) and

achromatic (luminance, or subjective “brightness”; ΔL) distances between color patches, with distances falling below a theoretical “threshold” (often referred to as a “just noticeable distance”) likely to represent patches that are near indistinguishable to the viewer. These thresholds have been behaviorally validated in several species, albeit predominantly in bright conditions, including our hypothesized viewers. In such cases, a theoretical value of 1 is typically adopted as a tentative predicted limit to discrimination, which we also adhere to here (Kemp et al. 2015). More relevant to our focal hypothesis than the absolute value of estimated contrasts (which are context specific; Kemp et al. 2015), however, is the presence of a rank-order shift in frog conspicuousness against “adapted” and “nonadapted” backgrounds.

Following initial visual modeling, we estimated the conspicuousness of frogs against distinct backgrounds using a bootstrap procedure (Maia and White 2018). For a given run, we sampled points from each group (frogs and backgrounds) equal to the size of the original group, with replacement, and calculated the distance between the center of each distribution. We repeated this process 1,000 times, generating a distribution of subjective chromatic and achromatic distances between groups, from which we calculated a mean chromatic (ΔS) and achromatic (ΔL) distance and 95% confidence interval. We then inspected this interval

to predict the discriminability of groups in color space. As noted above, if the value contained or was entirely less than the threshold value of 1, then the patches were predicted to be indistinguishable to nocturnal viewers under ideal conditions (Siddiqi et al. 2004). Conversely, intervals lying above this threshold suggested that such color patches should be increasingly conspicuous to such viewers (Fleishman et al. 2016). We used the package *pavo* (ver. 2.9.0; Maia et al. 2019) in R (ver. 4.4.1; R Core Team 2024) for all spectral processing and visual modeling.

Results

Tree Frog Coloration and Background-Induced Color Change Experiment

The reflectance profile of frogs on leaf litter backgrounds showed a relatively desaturated reflectance, with a weak peak in the 540–550-nm range that was otherwise dominated by the contribution of longer wavelengths (>650 nm; fig. 3a). Frogs resting on grass were instead characterized by a sharp peak in the 540–550-nm (“green”) range, with a maximum reflectance of ~40%–50% (fig. 3b). Frogs that were translocated between distinct background substrates showed rapid color shifts. Specifically, frogs that moved from grass to leaf litter background showed a significant decrease in saturation (estimate = $2,578 \pm 590$, $t_{24} = 4.369$, $P < .001$) and

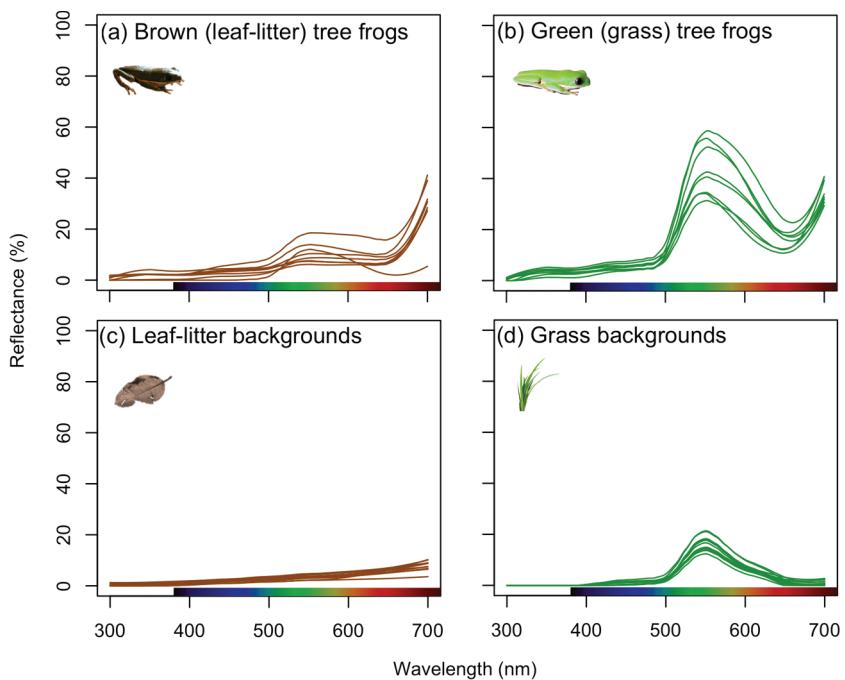


Figure 3: Reflectance spectra of frogs and substrates during dark-room experimental trials. Graph *a* depicts frog spectral reflectance after experimental individuals remained on a leaf litter background after 25 min, while *b* depicts frogs exposed to grass for 25 min. Graphs *c* and *d* depict spectral reflectance of background substrates leaf litter and grass, respectively. Photographs by Jaqueline Vaz da Silva.

an increase in their dominant wavelength (or “hue”; estimate = -87.2 ± 27.9 , $t_{24} = -3.126$, $P = .022$) over the 25-min period compared with those moved from grass to grass in the control treatment. We detected the opposite effect when moving individual frogs from leaf litter to grass substrates, with an increase in saturation (estimate = $-1,964 \pm 570$, $t_{24} = -3.446$, $P = .010$) and a decrease in the dominant wavelength toward the green region of the spectrum (estimate = -111.4 ± 27 , $t_{24} = -4.132$, $P = .002$), compared with those moved from leaf litter to leaf litter in the control treatment. In human terms, then, frogs became more “green” (or stayed green in the controls) when moved onto grass backgrounds. Conversely, they became more “brown” (or stayed brown in the controls) when moved to leaf litter backgrounds.

Tree Frog Conspicuousness to Putative Predators

We identified a distinct change in the subjective conspicuousness of frogs in response to background exposure.

However, the effect on contrasts varied according to the predator visual system. For trichromatic snakes, all frogs appeared better camouflaged in leaf litter than in grass, regardless of whether they were previously exposed to leaf litter or grass (fig. 4a, 4d). For mammals, the result was qualitatively similar, although the differences were less pronounced (fig. 4b, 4e). While for avians, leaf-litter-adapted frogs were predicted to be undetectable against this background but readily visible amid grass background. In parallel, leaf-litter-adapted frogs were predicted to blend in visually, although being relatively more visible against litter background (fig. 4c, 4f). For numerical details, see table S1 (available online).

For the achromatic visual channel, color changes in frogs from green to brown generate a significant decrease in contrast regardless of their backgrounds, whether grass or leaf litter (fig. 5a–5c for brown tree frogs; fig. 5e–5g for green tree frogs). However, individuals that turned brown had lower luminance contrasts on grass compared with leaf litter, so they are predicted to be indistinguishable

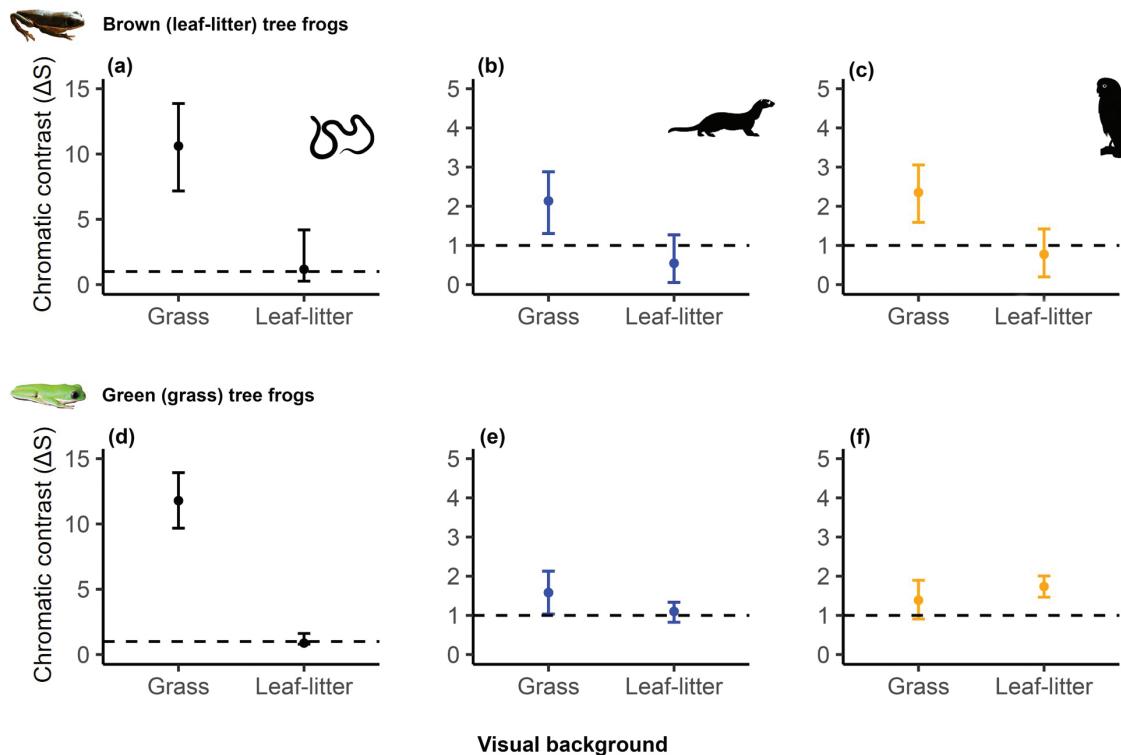


Figure 4: Chromatic (ΔS) contrasts of experimental *Pithecopus hypochondrialis* against their visual backgrounds considering the moon irradiance. Plots a–c show the color contrast of frogs for each predator type (snake [a], ferret [b], and owl [c]) of leaf-litter-adapted frogs compared with both visual backgrounds. Plots d–f show the color contrast of frogs for each predator type (snake [d], ferret [e], and owl [f]) of grass-adapted frogs compared with both visual backgrounds. Contrasts were modeled according to the visual threshold discriminability (dashed line) of the predators. Points and vertical lines represent mean values and the bootstrapped 95% confidence intervals.

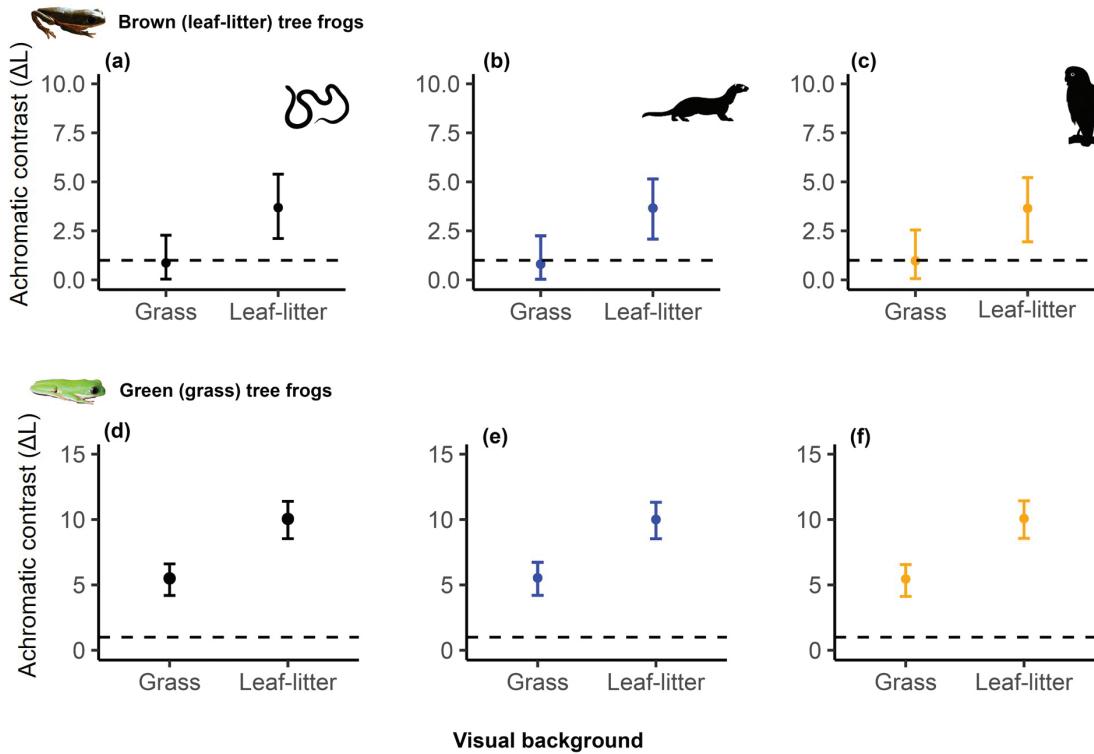


Figure 5: Achromatic (ΔL) contrasts of experimental *Pithecopus hypochondrialis* against their visual backgrounds considering moon irradiance. Plots *a–c* show luminance contrast of individuals for each predator type (snake [*a*], ferret [*b*], and owl [*c*]) when maintained over leaf litter backgrounds during the experiment and compared with both visual backgrounds. Plots *d–f* show the luminance contrast of individuals for each predator type (snake [*d*], ferret [*e*], and owl [*f*]) when maintained over grass backgrounds during the experiment and compared with both visual backgrounds. Contrasts were modeled according to the visual threshold discriminability (dashed line) of the predators. Points and vertical lines represent mean values and the bootstrapped 95% confidence intervals.

to all three focal predators, as they fall below the detection threshold.

Discussion

Our experiment on background-induced color change in *Pithecopus hypochondrialis* revealed a short-term physiological color change, which reduced their conspicuousness in a background-specific manner. Our findings are consistent with a hypothesis of dynamic nocturnal camouflage, although as discussed below, the demonstrated background matching is not predicted to be equally effective to all predators. Rapid color change is widespread in nature, seen, for example, in cephalopods, fish, chameleons, and amphibians (Figon and Casas 2018). In amphibians there is a gradient concerning the time required for color changes, ranging from rapid (minutes) to slow (weeks; Toledo and Haddad 2009). While color change in amphibians may also occur for thermoregulation purposes (Park et al. 2023), studies have shown an association between rapid color change in

cephalopods and amphibians with camouflage, including background matching and disruptive coloration (Mäthger et al. 2008; Hanlon et al. 2009; Kang et al. 2016).

Amphibians are preyed on by many groups of predators. Snakes, mammals, and birds are considered primary predators, with snakes accounting for the highest number of records (Toledo et al. 2007). We note that we lack direct evidence concerning the main predators of our focal anuran species and whether they primarily rely on vision or chemical cues. Thus, in our models, we included predators known to target anuran species more broadly. Differences in photoreceptor classes and properties influence how predators detect prey (Fennell et al. 2019). For example, a dichromatic mammal, such as a ferret, perceives green frogs on grass and leaf litter differently from predators with tetrachromatric or trichromatric vision, such as many birds and snakes (Jacobs 2009). Lacking medium-wavelength (green) photoreceptors, ferrets struggle to distinguish brown from green, whereas owls and snakes, which possess these receptors, perceive greater contrast between the frog and its backgrounds (fig. 4; Troscianko et al. 2017; Fennell

et al. 2019). Here, our visual modeling suggests that dynamic color change in *P. hypochondrialis* is most effective for camouflage against avian (e.g., owl) predators on both grass and leaf litter backgrounds. This accords with birds' visually driven foraging, while mammals and snakes rely on multiple, and predominantly nonvisual, sensory cues (Van Valkenburgh and Wayne 2010; Tadić 2023; Zdenek et al. 2023). Birds, making up 15% of predators on post-metamorphic frogs, have a well-studied and conserved visual system (Hart et al. 2001) and prey on at least 38 anuran species (Toledo et al. 2007). In Brazil predatory birds like the Strigidae family (including the tawny owl) are prevalent and known to prey on frogs, especially in the Cerrado savanna (Sick 2001; Vieira et al. 2015). The understanding of vertebrate vision mainly stems from studies on specific mammals, birds, and fish (Nickle and Robinson 2007; Simões et al. 2016). Snake vision, however, is diverse and underexplored, particularly among the Colubridae family. Here, we used the visual phenotype of the diurnal garter snake (*Thamnophis sirtalis*), acknowledging limited knowledge on snake visual systems. Snakes may be best suited to detect green frogs in grass, while birds and mammals might struggle more with color differentiation.

The background substrate switch did not induce background-specific differences in achromatic contrast for either green or brown frogs on grass or leaf litter. For brown frogs, however, we observed a pronounced reduction in said contrast, particularly when viewed against grass, which was consistent across all predators. This is likely to be useful when viewed over long distances, since this visual channel guides stimulus detection at medium and long distances (Osorio et al. 1999; but see Kelber et al. 2003). Indeed, this reduction in achromatic contrast should confer advantages during ground movements even in the presence of potential predators, since grass constitutes the predominant substrate within the ponds. This finding is also consistent with past work showing that achromatic changes are often particularly pronounced among animals that bear dynamic color signals, which can vary from conspicuous during social interactions to cryptic, depending on environmental cues (Stegen et al. 2004; Whiting et al. 2022).

Nocturnal illumination is subject to temporal fluctuations and varies significantly between different locations, such as urban versus natural habitats and areas with dense versus sparse canopy cover. These variations in light conditions can impact the ability of predators to detect and distinguish *P. hypochondrialis* in various ways. Nevertheless, our modeling suggests that despite differences in nighttime irradiance, including the presence of a full moon and starlight, there was no discernible alteration in the overall outcome. That is, variation in nocturnal illumination is unlikely to strongly shape predators' capacity to detect prey across the diverse backgrounds

tested. Unlike Kang et al. (2016), which inserted frogs in different color and patterning background and measured the frogs after a nighttime acclimation period (i.e., each day, a frog underwent testing exclusively against a single background type), our experiment showed that *P. hypochondrialis* are capable of performing multiple rapid color changes during nocturnal conditions, thereby adjusting their coloration to reduce contrast depending on their background. However, following Kang et al. (2016), it is plausible that nocturnal color changes in *P. hypochondrialis* could similarly provide camouflage benefits not only at night but also at dawn, dusk, and even during daylight hours. Animals are capable of identifying predation risks and adjust their behavior to avoid predators, such as altering habitat use or, in some situations, drastically altering their coloration. A recent study showed that Jackson's chameleons (*Trioceros jacksonii xantholophus*), in their natural range (Kenya), are capable of changing their color to become even more cryptic when predators are present (Whiting et al. 2022). Although not related to chameleons, nocturnal frogs might use other cues to match their coloration and luminance to the substrate on which they rest. We suggest that further studies should be carried out to elucidate which environmental cues in nocturnal environments, such as predator vocalization or chemical cues, can induce color changes in *P. hypochondrialis*.

Considering the lack of information on the natural history of this species, especially regarding nocturnal behavior and predator-prey interactions, a central question remains unresolved: why is color change important at night? We suggest here that color change may be significant in avoiding nocturnal predators, such as birds and mammals, in specific backgrounds. Additionally, we propose that this change may be important during twilight, where various predators are active and lighting can be more intense. Nocturnal habits promote biodiversity because of habitat segregation and species coexistence in the wild (Begon 2021). With this in mind, studies that elucidate the natural history of nocturnal animals could significantly enhance our ability to understand how the biodiversity of understudied nocturnal species, as well as predator-prey interactions, evolve and are shaped during nighttime. Furthermore, we suggest investigating the role of camouflage in combination with the bright orange coloration of the legs, which remains hidden while the frog is at rest but may potentially act as a distraction strategy when the frog is disturbed by predators, increasing its chances of escape. Our findings highlight the importance of rapid nocturnal color change as a short-term physiological mechanism of camouflage in tropical amphibians against diverse predators. We suggest new experimental studies to understand the impact of color change on predation rates for each predator type, as well as experiments

regarding the main sensory systems used by predators to locate and prey on these frogs.

Acknowledgments

We thank Natural History Editor Leticia Avilés, the anonymous reviewers, and Data Editor Benedicte Bachelot for their thorough corrections and valuable suggestions to improve our article. We are also grateful to Gustavo Q. Romero, Vinicius L. G. Brito, Yuri F. Messas, João Vasconcellos Neto, and Marcelo O. Gonzaga for their insightful comments, support, and constructive feedback. We acknowledge the Universidade Federal de Uberlândia and the Reserva Ecológica do Panga for their support and for granting permission to conduct the fieldwork. This work was funded by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (J.V.d.A.V., grant 88887.338483/2019-00), the Graduate Program in Ecology, the Instituto de Biologia, and the Universidade Estadual de Campinas (UNICAMP). All capture and handling of individuals of *Pithecopus hypochondrialis* were approved by the competent Brazilian legislation (SISBIO 86439-1) and the university ethics committee (Comissão de Ética no Uso de Animais/UNICAMP: 6158-1/2022). All individual tree frogs were released at their capture location immediately after the short restraining period.

Statement of Authorship

J.V.d.A.V., R.V.S.G., P.P.R., and J.V.d.S. conceived and designed the study and conducted the fieldwork. T.E.W. and J.V.d.A.V. analyzed the data. T.E.W. and C.G.B. supervised the research. C.L. critically revised the manuscript for submission. All authors read and approved the final version of the manuscript.

Data and Code Availability

All data from this study are available on figshare (<https://doi.org/10.6084/m9.figshare.24045684>; de Alcantara Viana et al. 2025).

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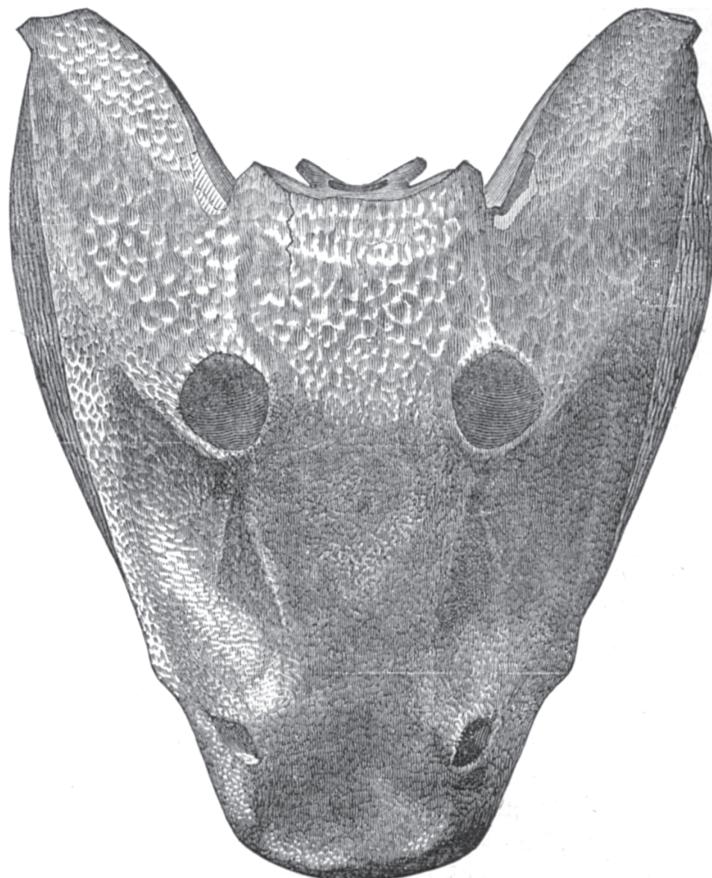
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Natural History Editor: Leticia Avilés



"This is the largest American batrachian, the skull measuring a foot wide by eighteen inches long. It was very abundant, constituting with the reptilian genus *Dimetrodon*, the most prominent type of the Permian fauna in this country." Figured: "*Eryops megacephalus* Cope." From "The Batrachia of the Permian Period of North America" by E. D. Cope (*The American Naturalist*, 1884, 18:26–39).