Behavioral Correlates of Coloration in Tropical Anurans

By: Justin Looper

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Thesis Advisor: Dr. J. Rinehimer

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I pledge my word of honor that I have abided by the Washington College Honor Code while completing this assignment



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Abstract

Crypticity and aposematism have evolved within many anuran species as defensive strategies built on adaptive coloration. Behavior plays a key role in the effectiveness of each strategy. However, the true extent of the relationship between conspicuousness and behavior within and between species remains unclear. This study seeks to understand the relationship between coloration and behavior in tropical anurans using escape behavior and contrast with substrate as a measure of conspicuousness. Aposematic individuals exhibited farther flight initiation distances, more short hops and fewer long hops, wider escape angles, less refuge seeking behavior, and higher contrast with substrate than cryptic frogs. However, individual contrast did not appear to have a substantial effect on escape behavior. These results suggest behavior is innate and is not correlated with individual contrast intensity. This study builds upon past research regarding the adaptive behavior associated with coloration and provides new context for individual intensity-dependent behavior.

Introduction

Visual systems are one of the most common methods predators use to find prey, particularly in predator groups with well-developed color vision, such as birds (Simmons, 2009). Consequently, groups of organisms whose predators rely primarily on sight have evolved defensive mechanisms based on adaptive coloration (Simmons, 2009). Two main types of adaptive coloration, including disguise and advertisement, have since been major realms of study within animal morphology and behavior (Bond, 2007; Rojas et al., 2015).

Crypsis describes a form of adaptive coloration achieved by background matching, in which an organism seeks out a position in the substrate that matches their coloration (Bond, 2007). Conversely to crypsis, advertisement, also commonly known as aposematic coloration, or warning coloration, describes conspicuous coloration or behavior meant to convey unprofitability to a potential predator (Rojas et al., 2015). Typically, this characteristic is associated with a degree of unpalatability in the organism, commonly in the form of toxins or distasteful substances (Poulton, 1980; Rojas et al., 2015). Both forms of adaptive coloration confer antipredator benefits. Crypticity reduces the likelihood of detection by a predator, while aposematic coloration encourages avoidance by predators (Bond, 2007; Rojas et al., 2015). These morphological traits, combined with other factors such as micro-habitat selection can be key to an organism's survival (Paluh et al., 2014; Oliveira et al., 2020).

Of the two types of adaptive coloration, the evolutionary roots of crypticity are better understood than that of aposematism. The combination of predator-prey interactions and geography have shaped cryptic organisms' morphology over evolutionary time to best increase their chance of survival within their environment. Crypticity is widely understood to be an instance of coevolution between predator searching capabilities and the degree of prey

camouflage (Bond, 2007; Struck, 2018). As predator searching mechanisms evolve, prey species similarly develop better abilities to hide from and disrupt a predator's search image. Additionally, crypticity often promotes polytypic populations, as geographically isolated species have evolved coloration to take advantage of specific local predators' visual processing (Bond, 2002).

The evolutionary mechanisms of aposematic coloration are less understood than that of crypticity, giving rise to the aposematic evolution paradox. This addresses the logical constraints on the evolution of aposematism, as new conspicuous phenotypes would be more prone to predation and thus would not benefit from their distastefulness (Mallet & Singer, 1987). Furthermore, an aposematic mutant would be selected against in a homogenous population, likely not passing on its genes (Leimar et al., 1986). There are a few lines of evidence that could explain the evolution of conspicuous coloration despite the clear restraints. One such possibility argues that the evolution of aposematism is facilitated by the restraints of cryptic coloration, particularly in diurnal species. Merilaita and Tullberg (2005) demonstrated this idea through Lepidopteran evolutionary simulations and found that adaptive colorations evolved at least once in each day-active group and never in closely related nocturnal species. As such, the costs associated with reduced daytime motility in a heterogeneous environment may have favored the speciation away from cryptic coloration toward aposematism (Merilaita & Tullberg, 2005).

The evolution of aposematism as a successful strategy may also be attributed to predator learning from repeated encounters with unpalatable, conspicuous prey. One proposed mechanism is "go slow" behavior, in which a predator exhibits caution when encountering unfamiliar prey, resulting in higher escape and survival chance in a conspicuous individual (Coppinger, 1980). A second mechanism–"resource allocation trade-off"–refers to how color intensity can be an honest

display of toxicity (Maan & Cummings, 2012). A higher level of toxicity is associated with a higher degree of predator learning from an unpalatable predation attempt; predators of aposematic individuals would learn to associate brightness with unprofitable prey. These two proposed mechanisms define how predator learning could possibly facilitate the evolution of aposematism (Holen & Svennungsen, 2012).

Aposematism may have also evolved due to social interactions with conspecifics. Individuals aiding their relatives in survival and reproduction favors altruistic behaviors that ensure that shared genes are passed on (Michod, 1982). Group living tends to be more common in aposematic populations, leading to increased relatedness between conspecifics where aposematic traits would emerge in several individuals at once, thus favoring kin selection. A predator samples one distasteful individual, leading to avoid other aposematic individuals and thus increasing prey fitness (Järvi et al., 1981).

Sexual selection may also drive conspicuous coloration and toxicity, complementing predator-driven selection, strengthening the evolution of aposematic, chemically defended phenotypes. There is evidence that the intensity of conspicuous coloration can be an honest signal of fitness, as female poison dart frogs select for more conspicuous males (Maan & Cummings, 2009; Dreher et al., 2015). Furthermore, in aposematic Dendrobatid *Oophaga pumilio*, toxicity has been shown to be positively correlated with dorsal brightness (Maan & Cummings, 2012). Together, these findings support the idea that color intensity serves as an indicator of fitness, an 'honest signal' that females select for in males with more advantageous genes to pass on to their offspring. Despite this, the evolution of aposematic coloration cannot be accredited to a single mechanism and is likely a combination of factors.

Aposematism is not universally more advantageous than crypticity. Environmental factors, such as substrate and amount of refuge, can influence the relative effectiveness of warning signals, and prey strategy can differ by location and predator communities. As a result, selective pressures may favor either crypticity or aposematism across ecological contexts (Briolat et al., 2019). Factors such as predator visual acuity, vulnerability to toxin, and differences in sensory processes encourage either crypticity or aposematism in populations (Guilford & Stamp, 1991; Mappes et al., 2005; Osorio & Vorobyev, 2008).

Prey behavior plays a crucial role in maximizing the effectiveness of coloration. Cryptic individuals increase their crypticity via immobility, while aposematic individuals increase their conspicuousness through movement, effectively signaling their unprofitability (Blanchette et al., 2017). Even within *Oophaga pumilio*, more conspicuous individuals exhibit greater activity than less conspicuous morphs (Pröhl & Ostrowski, 2011). Additionally, some species have a demonstrated ability to cognitively select backgrounds that increase their level of crypticity (Briffa et al, 2008; Kang et al., 2012). Furthermore, microhabitat position, including substrate type and background color, influences individual behavior and causes individuals to move differently based on their crypticity (Heinen, 1985; Oliveira, el al., 2020). An individual might crawl slowly while it is well hidden in a dark substrate but jump quickly when it has high contrast with a light substrate. These substrate-dependent strategies work in tandem with individual coloration to influence predator detection rate.

Clear patterns can be drawn between behavior and degree of conspicuousness, yet previous studies have focused on either intraspecific or interspecific comparisons (Pröhl & Ostrowski, 2011; Gray, 2023). While revealing broad trends between movement behavior and coloration, they have yet to conclude whether these patterns are present at the community level.

Additionally, it is unclear if activity level is directly correlated with individual brightness. This study seeks to understand the relationship between degree of conspicuousness and escape behavior across a range of tropical Anuran species, using contrast with substrate as a measurement of conspicuousness (Dreher et al., 2015). These data will allow conclusions to be drawn about how behavior is correlated to adaptive coloration as a whole, ruling out species-specific behavioral adaptations.

Methods

This study was conducted in Costa Rica over the course of two weeks from January 1st to 13th, 2026. Individuals were sampled from two biological stations: La Suerte Biological Field Station in Limón and La Selva Biological Station in Heredia. Both locations contained several hundred acres of lowland tropical rainforest, with large populations of *Oophaga pumilio* (strawberry poison dart frog), *Dendrobates auratus* (green and black poison dart frog), and cryptic frog species such as *Engystomops pustulosus* (túngara frog) or *Rhaebo haematiticus* (leaf litter toad).

Observations occurred during the day and at night along the trails at both locations. When a frog was located along the trail, the observer stopped moving and watched the individual until it stopped moving. The frog was given 30 seconds to acclimate to the presence of the observer before the behavioral analysis began (Blanchette et al., 2017). An observation was abandoned if the individual did not remain motionless for more than 30 seconds or moved out of view.

Four behaviors were recorded for each frog observed: flight initiation distance, number of jumps, escape angle, and refuge-seeking behavior. After the frog had acclimated, the observer positioned themselves so that there was at least 2 meters between them and the frog. The observer then placed a flagging tape marker at their feet to indicate starting distance before beginning to move towards the frog in a straight line, taking one step each second (Gray et al., 2023). Movement towards the frog continued until the frog initiated escape, at which point a second flagging tape marker was placed at the foot of the observer. The distance (cm) between the starting location of the frog and the second marker was defined as the flight initiation distance, a useful metric of fear response and level of perceived risk in organisms. The distance between the starting location of the frog and the first marker was defined as the starting distance.

Standardized flight initiation distance was calculated as flight initiation distance divided by starting distance. Standardized flight initiation distance was used as the metric of escape response for each frog, as starting distances were not equal among behavioral assays. If the frog did not escape when the observer was within 30 cm, the observer took a paintbrush and slowly moved it towards the frog, brushing the frog on its dorsal surface once. If the frog did not escape even after it was stimulated, the flight initiation distance and number of jumps was considered 0, and the angle of escape and refuge-seeking behavior was not measured (Blanchette et al., 2017).

After escape began, I recorded the number of jumps a frog took before it remained motionless for 5 seconds or was out of view (Blanchette, 2017). Each jump was recorded as either a small jump (<5cm) or a large jump (>5cm). Secondly, the angle of escape was measured on a range from 0-180°, with 0° being directly away from the direction of approach and 180° being directly toward the direction of approach. Angle of escape was categorized as one of the following angles: 0°; 25°; 45°; 75°; 90°; 115°; 135°; 165°; or 180°. It was not possible to measure the precise angle of escape. Direction left or right was not considered, so a frog jumping left or right perpendicularly to the direction of approach would both be considered a 90° escape angle. Lastly, I indicated whether or not the frog used refuge-seeking behavior by recording whether the frog was visible after it stopped moving.

A photograph was taken of each frog sampled at the beginning of each behavioral observation for later contrast analysis. All images were captured using a Canon EOS Rebel T7 through a 55-300mm lens at a minimum distance of 2 meters. To standardize lighting conditions at night, a second observer illuminated the frog using a flashlight positioned 2m away at a 45° angle relative to both the frog and the camera.

Contrast between the individual frog and the substrate (conspicuousness) was measured in ImageJ as the absolute value of the difference in weighted pixel intensity between the frog and its surrounding substrate. The frog's shape was outlined in ImageJ, and the mean weighted intensity within this outline was recorded as the frog's color intensity. The outline was then moved to an area on the individual's most immediate substrate within 5 cm, and the mean pixel intensity in this region was recorded as the substrate's color intensity. The absolute value difference between these values served as the conspicuousness for each frog. This procedure was applied to the total weighted color intensity (combined red, green, and blue channels) as well as to each individual color channel for every frog.

Data were analyzed based on three groups: *Oophaga pumilio* (strawberry poison dart frog), *Dendrobates auratus* (green and black poison dart frog), and all cryptic frogs. Data for standardized flight initiation distance, number of small jumps and large jumps, and angle of escape were analyzed in Excel using ANOVA single factor and multiple comparisons test with $p<0.05$ as the threshold for statistical significance.

Results

A total of 99 individuals were sampled across both sites, with 94 at La Suerte and 5 at La Selva. Of the 99 total observations, 90 occurred during the day, with the remaining 9 occurring at night. There were 69 *O. pumilio*, 11 *D. auratus*, and 19 cryptic individuals of 9 species observed. The cryptic species distribution was as follows: 3 *Craugastor bransfordii* (Bransford's litter frog), 4 *Craugastor megacephalus* (atlantic broad-headed litter frog), 2 *Craugastor polyptychus* (coastal plain litter frog), 4 *Leptodactylus melanotus* (sabinal frog), 2 *Rhinella horribilis* (giant toad), and single individuals of *Leptodactylus savagei* (Savage's thin-toed frog), *Pristimantis cerasinus* (clay-colored rain frog), *Rhaebo haematiticus* (leaf litter toad), and *Scinax staufferi* (Stauffer's tree frog). Frog-substrate contrast was significantly higher in *O. pumilio* and *D. auratus* individuals than cryptic individuals ($p<0.001$) but was not significantly different between *O. pumilio and D. auratus* individuals ($p=0.075$; Table 1, Figure 1) Average frog-substrate contrast in *D. auratus* was 38.3% higher than *O. pumilio* and 248.1% higher than the cryptic average. The *O. pumilio* average for frog-substrate contrast was 151.6% higher than the average for cryptic individuals.

Table 1 Escape behavior and contrast in tropical anurans. Standardized flight initiation distance (SFID) is used as a metric of individual fear response and perceived threat level, measured as the distance at which the individual initiated flight divided by the starting approach distance. Data is arranged as mean±standard deviation.

Species	Average Contrast (pixel difference)	Average SFID	Average small hops (#)	Average large hops (#)	Average escape angle	% sought refuge
O. pumilio	34.5 ± 21.9	31.3 ± 22.3%	2.26 ± 1.5	0.32 ± 0.6	46.7°	40.6%
D. auratus	47.7 ± 26.6	44.8 ± 19.2%	1.91 ± 1.0	0.18 ± 0.4	42.3°	0%

Cryptic	13.7 ± 17.5	4.6 ± 8.7%	0.26 ± 0.6	1.16 ± 1.1	15.9°	76.5%

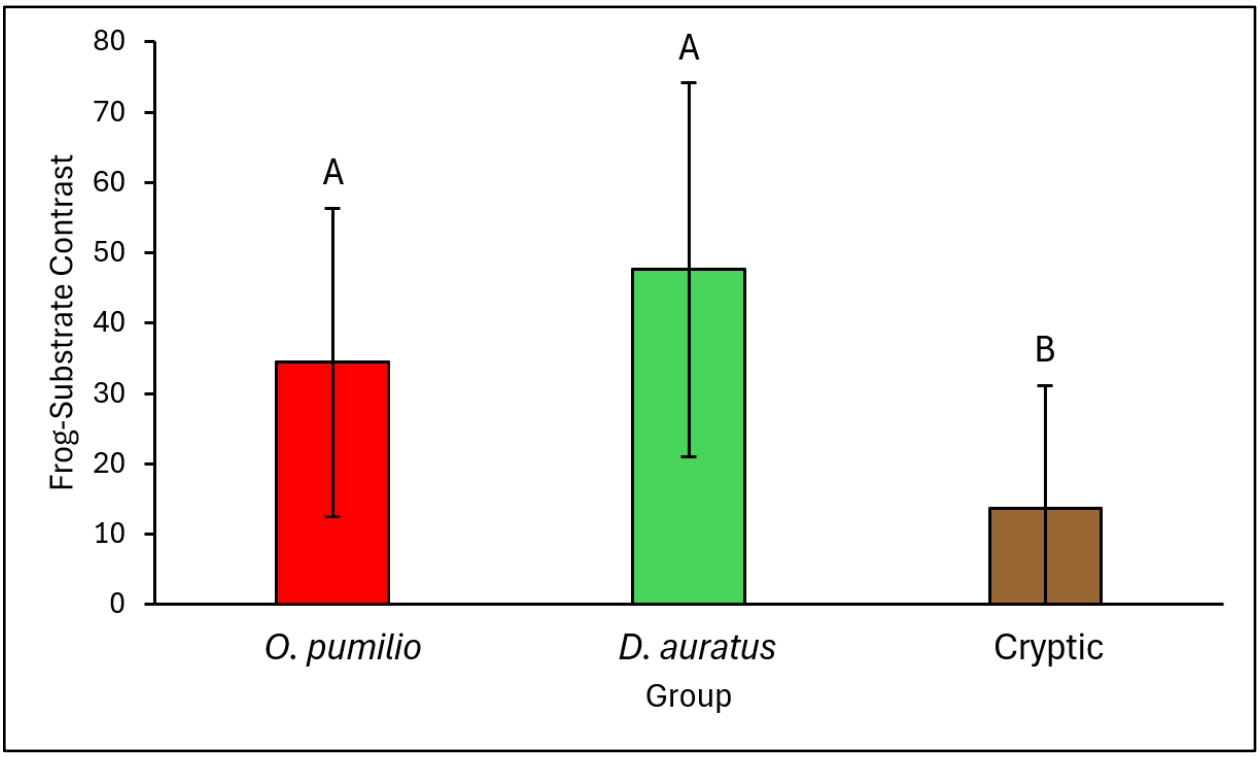


Figure 1 Contrast with substrate in tropical anurans. Frogs were photographed at a distance of at least 2 meters with standardized lighting. Individuals were grouped into three categories: *Oophaga pumilio* (N=67); *Dendrobates auratus* (N=11); and all cryptic species (N=19). Contrast was measured in ImageJ as the absolute value of the difference in weighted pixel intensity between the frog and its surrounding substrate. Letters above the bars indicate a significant difference from groups that do not share the same letter (P<0.01). Error bars indicate standard deviation.

O. pumilio and *D. auratus* individuals exhibited significantly higher standardized flight initiation distance than cryptic individuals ($p<0.0001$), but not from each other ($p=0.075$, Table 1, Figure 2). This means that individuals of *O. pumilio* and *D. auratus* initiated flight sooner, and that the observer was able to get closer to cryptic individuals before they began fleeing. Average standardized flight initiation distance in *D. auratus* was 40.1% higher than the *O. pumilio* average, and 884.8% higher than the cryptic average. The *O. pumilio* average for standardized flight initiation distance was 601.5% higher than for cryptic individuals.

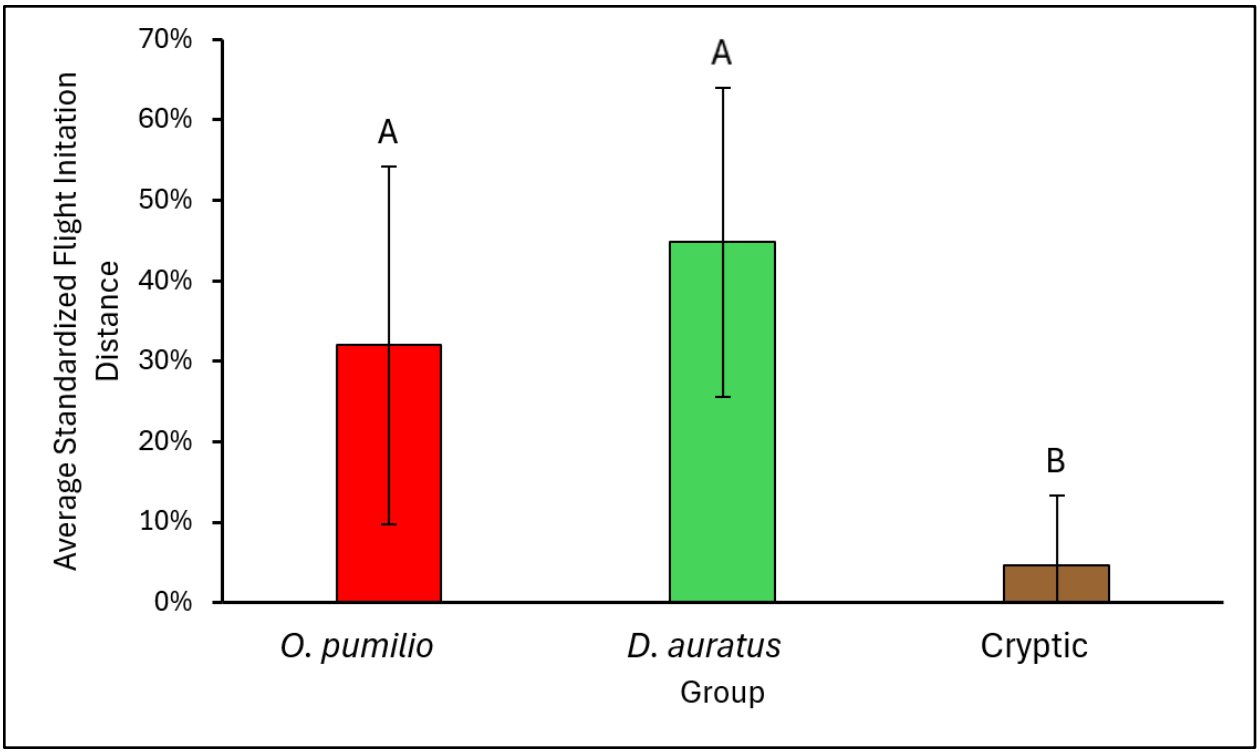


Figure 2 Flight initiation distance in tropical anurans. Frogs were approached by an observer from a distance of at least 2 meters. Standardized flight initiation distance was measured as the proportion of starting distance at which the frog initiated escape.Individuals were grouped into three categories: *Oophaga pumilio* (N=69); *Dendrobates auratus* (N=11); and all cryptic species (N=19). Letters above the bars indicate a significant difference from groups that do not share the same letter (P<0.0001). Error bars indicate standard deviation.

O. pumilio and *D. auratus* individuals made more short hops on average than cryptic individuals ($p<0.0001$), but not from each other ($p=0.46$, Table 1, Figure 3). *O. pumilio* performed 769.2% more short hops on average than the cryptic species. *D. auratus* individuals performed 634.6% more short hops on average than cryptic individuals. Cryptic individuals performed significantly more long hops on average than individuals of *O. pumilio* ($p<0.0001$). Cryptic individuals performed 254.9% more long hops on average than *O. pumilio* individuals and 531.9% more than *D. auratus* individuals. Additionally, both *O. pumilio* and *D. auratus* used significantly more short hops than long hops ($p<0.0001$), with *O. pumilio* and *D. auratus* performing 597.5% and 961.1% more short hops on average, respectively.

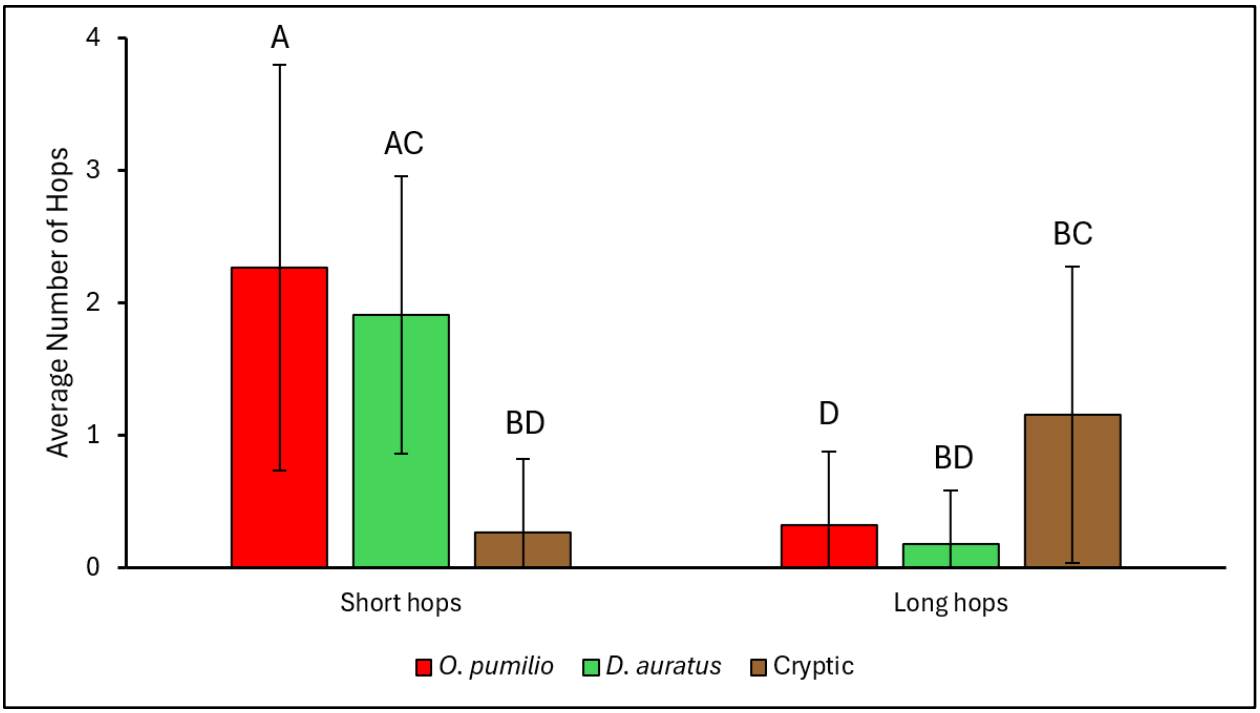


Figure 3 Escape behavior in tropical anurans. Frogs were approached by an observer from a distance of at least 2 meters. The number of hops was counted after flight was initiated, with each categorized as either a short hop (<5cm) or a large hop (>5cm). Individuals were grouped into three categories: *Oophaga pumilio* (N=69); *Dendrobates auratus* (N=11); and all cryptic species (N=19). Letters above the bars indicate a significant difference from groups that do not share the same letter (P<0.05). Error bars indicate standard deviation.

The average escape angle was the sharpest in cryptic individuals and the widest in *O. pumilio* individuals, with individuals of *O. pumilio* escaping at significantly sharper angles than cryptic individuals ($p<0.001$, Table 1, Figure 4). The average escape angle for *O. pumilio* individuals was 46.7°, 10.4% higher than the average for *D. auratus* individuals of 42.3° and 193.7% higher than the average for cryptic individuals of 15.9°.

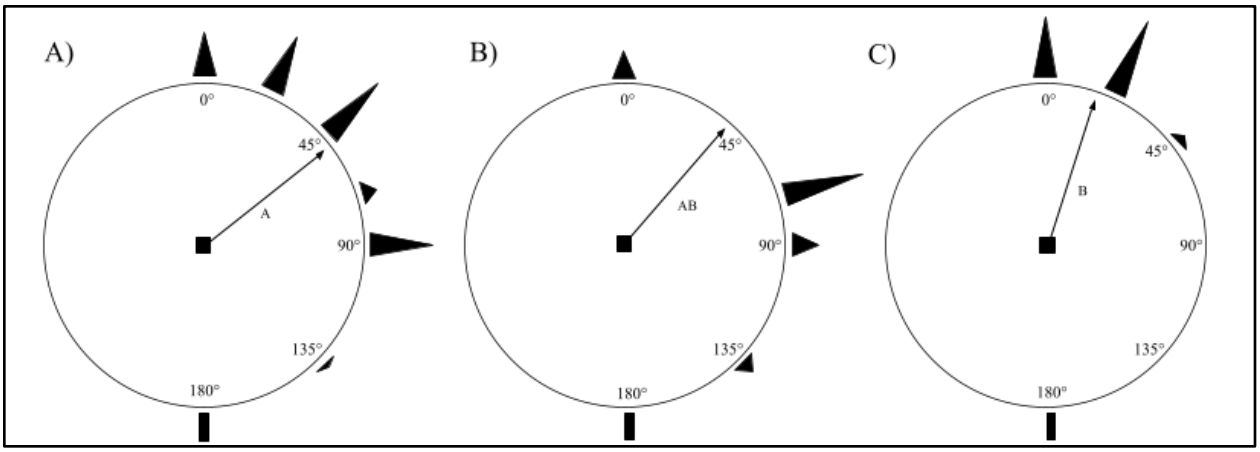


Figure 4 Escape angle in tropical anurans. Frogs were approached by an observer from a distance of at least 2 meters. Angle of escape was measured on a scale of 0-180° after flight was initiated. The square in the center of the circle indicates the starting position of the frog, with direction of approach by the observer represented by the rectangle beneath the circle. The arrow for each panel represents the average escape angle for each group, with the triangles around the circle proportionally representing the number of individuals that escaped in that direction.Individuals were grouped into three categories: *Oophaga pumilio* (N=69); *Dendrobates auratus* (N=11); and all cryptic species (N=19). Letters next to arrows indicate a significant difference from groups that do not share the same letter (P<0.05).

A greater number of cryptic individuals sought refuge than *O. pumilio* or *D. auratus* individuals (Table 1, Figure 5). Only 40.58% of *O. pumilio* individuals were not visible after flight, compared to 76.47% of cryptic individuals. Zero *D. auratus* individuals sought refuge.

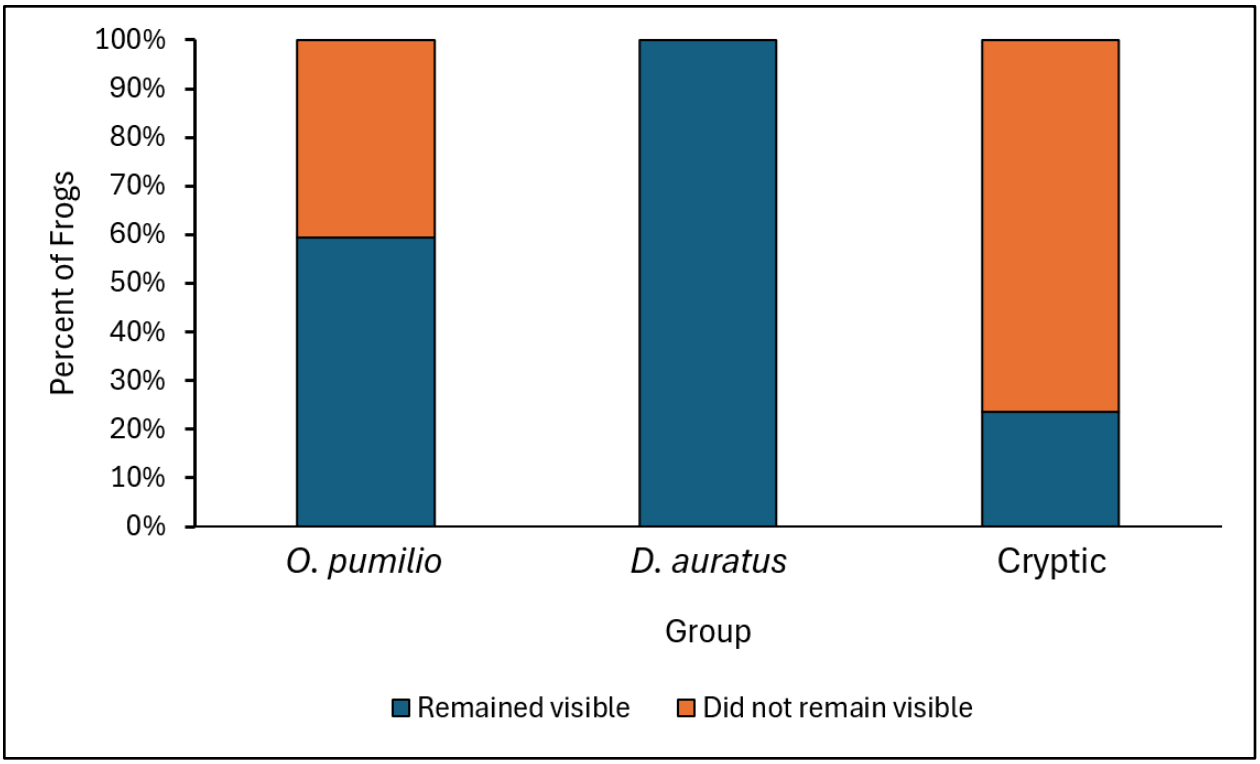


Figure 5 Refuge seeking behavior in tropical anurans. Frogs were approached by an observer from a distance of at least 2 meters. Individuals were observed until they stopped moving or were no longer visible. Individuals were grouped into three categories: *Oophaga pumilio* (N=69); *Dendrobates auratus* (N=11); and all cryptic species (N=19).

Frog-substrate contrast did not have a substantial effect on standardized flight initiation distance within groups (Table 1, Figure 6). Standardized flight initiation distance had a slightly negative relationship with frog-substrate contrast in *O. pumilio* and cryptic individuals, with linear trends of -0.04x+33.84 and -0.04x+5.13, respectively. In *D. auratus* individuals, standardized flight initiation distance had a slightly positive relationship, with a linear trend of 0.07x+41.47. Among all groups, standardized flight initiation distance displayed a positive relationship with frog-substrate contrast with a linear trend of 0.2x+21.98.

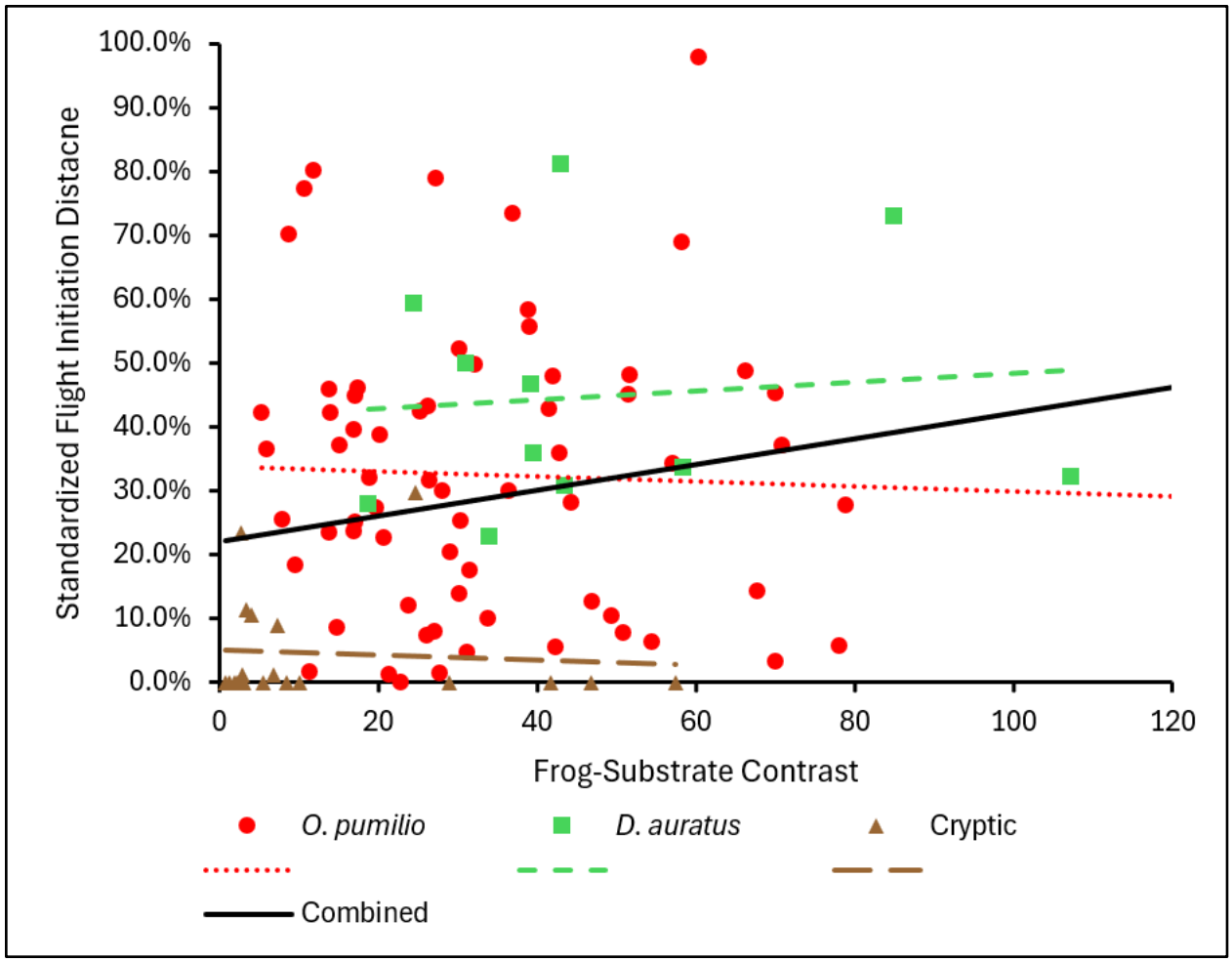


Figure 6 The effect of frog-substrate contrast on flight initiation distance in tropical anurans. Standardized flight initiation distance was measured as the proportion of starting distance at which the frog initiated escape. Frog-substrate contrast was measured in ImageJ as the absolute value of the difference in weighted pixel intensity between the frog and its surrounding substrate. Individuals were grouped into three categories: *Oophaga pumilio* (N=67); *Dendrobates auratus* (N=11); and all cryptic species (N=19). The trendline for each group represents the linear trend for that group. The black trendline indicates the linear trend for all samples.

Discussion

These results illustrate a clear relationship between escape behavior and adaptive coloration in tropical anurans. Aposematic individuals acted significantly differently than cryptic individuals when approached by an observer and employed bold behavioral strategies that maximized the effectiveness of their warning signals. Both aposematic species initiated flight earlier during predator approach (Table 1, Figure 2). Because aposematism relies on a predator's ability to visually identify conspicuous colors that they have learned to avoid, earlier flight initiation may increase the probability that these signals are perceived (Paluh et al., 2014; Blanchette et al., 2017). Furthermore, the use of shorter hops and escaping at a wider angle keeps the individual within the predator's visual field, as immediate fleeing could encourage pursuit by the predator, incurring energy costs and possible predation if warning signals are not properly conveyed (Figure 3; Figure 4; Gray et al., 2023). This statement is supported by the observation that the majority of aposematic individuals did not seek refuge, despite a leaf litter microhabitat with plenty of opportunities for cover (Figure 5). Similar escape behavior has been shown in Dendrobatid frogs in past research, highlighting the reduced escape behavior characteristic of this family (Cooper et al., 2009; Ozel & Stynoski, 2011; Blanchette et al., 2017). These results suggest that aposematic species utilize bold escape behavior to enhance conspicuousness, and subsequently the transmission of warning signals.

Unlike aposematic frogs, cryptic individuals favored shy escape strategies. Cryptic individuals did not initiate flight until the observer was much closer to them, relying on their crypticity and background matching to decrease a predator's chances of seeing them (Table 2; Cooper et al., 2008). Only when the observer was extremely close did the individuals initiate flight, choosing either to hide again or to use long hops in the opposite direction to put distance

between the observer and the frog. Both strategies initially rely on the camouflage provided by their coloration, secondarily choosing a tactic that forces a predator to expend energy continuing to search for or chase after them. Cooper et al. (2008) and Blanchette et al. (2017) observed similar behavior in cryptic *Craugastor* species. These results suggest that cryptic species utilize immobility to enhance their crypticity and avoid detection by predators (Blanchette et al., 2017).

Decreased predation rate might not be the sole motivator in the differentiation between aposematic and cryptic escape tactics. The evolutionary origins for this divergence in behavior may instead be rooted in the energy costs of the different strategies. Cryptic individuals pay high costs imposed by immobility, including decreased foraging, thermoregulation, and communication opportunity (Speed & Ruxton, 2005). As such, aposematism likely evolved with chemical defenses as a way to exploit more opportunities in the environment, as immobility was no longer necessary to avoid predation. These costs of crypsis negated by aposematism likely facilitated the evolution of bold behavior in aposematic individuals (Merilaita & Tullberg, 2005).

A similar pattern has been observed in three sexually dimorphic *Habronattus* jumping spider species, in which the aposematic males spend more time moving compared to cryptic females (Taylor et al., 2019). Similarly, the evolution of bold behavior likely evolved with increased activity levels in aposematic individuals as a way to offset the high energy costs of being aposematic (Speed et al., 2010). As toxicity and color intensity is directly correlated with diet, access to resources is an important factor in determining the effectiveness of aposematism (Flores et al., 2013). Aposematic individuals must spend a large amount of time foraging to maintain an effective level of toxicity and brightness, thus high activity level and boldness is selected for as a method to facilitate that.

These results also provide context for the determinants of behavior in aposematic and cryptic individuals. The biggest factor influencing escape behavior in tropical anurans appears to be adaptive coloration. Aposematic species and cryptic species used significantly different strategies in all escape metrics. Additionally, *O. pumilio* individuals and *D. auratus* individuals resembled each other in escape behaviors, implying a lack of species specific strategy determination. Furthermore, there is no evidence of individual behavior being affected by that individual's substrate contrast intensity (Figure 6). Regardless of their current level of conspicuousness, aposematic individuals behaved in a manner that increased their conspicuousness, while all cryptic individuals did the opposite.

The absence of a relationship between individual substrate contrast and flight initiation distance can be interpreted several different ways. Maan & Cummings (2012) demonstrated that individual brightness is positively correlated with toxicity. However, individual brightness may be selected for an honest signal to mates, rather than enhancing warning signals to predators (Maan & Cummings, 2009; Maisonneuve & Aubier, 2025). The bright pigments associated with aposematism also play an important role in immune health and fighting off parasites (de Roode & Groot, 2025). Serving as an honest signal, females select for bright males as a signal of health and fitness, more so than survivability. The existence of Batesian mimics implies the relative importance of toxicity compared to phenotypic similarity in effectively deterring predators. Furthermore, in the visual transmission of warning signals, pattern may be a more important signal than color intensity (Wüster et al., 2004).

Individual variation in escape behavior in these tropical anurans may be mediated by several other factors rather than individual contrast intensity. There is evidence that escape behavior may exhibit plasticity based on certain conditions, such as environment, individual

condition, and past experiences, a phenomenon studied in a variety of organisms such as teleosts and Orthopterans (Domenici, 2010; Ramasamy et al., 2015; Mitra et al., 2026). Predator type and prey sex as a determinant of escape behavior are well studied concepts (Blanchette et al., 2017). Instances of heritable as well as age-dependent variations escape behavior have also been observed (Heinze, 1974; Brokordt et al., 2012). Furthermore, social learning of escape behavior occurs in species of fish, sharks, and larval amphibians (Nadler et al., 2010). It is possible that any combination of these factors could play a role in variation in escape behavior among individuals of tropical anurans. In *O. pumilio* specifically, escape response to humans has been shown to differ from escape response to other, more natural predator types (Cooper et al., 2009, Ozel & Stynoski, 2011; Blanchette et al., 2017). This could possibly confound the data presented in this study. As such, future iterations of this study should consider the use of more natural and variable predator simulations.

This study builds upon previous studies comparing the escape behavior associated with aposematic species and provides context for individual intensity-dependent behavior. A previously poorly understood relationship, escape behavior appears to be primarily determined by adaptive coloration and not individual color intensity. A larger sample size may serve to reduce variation and increase the precision of this data, possibly revealing new, stronger trends. Additionally, focusing observations on either night or day behavior could eliminate the presence of time of day variations in behavior. These findings have broader implications for the study of adaptive coloration and escape behavior, highlighting key motivators and the importance of behavior in antipredator strategy. Further research into the association between individual contrast and escape behavior is required to understand the complexity of this relationship.

Another future line of questioning lies in exploring the underlying cause of variation in individual behavior within these groups from both a proximate and evolutionary perspective.

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