Evolutionary Ecology
https://doi.org/10.1007/s10682-023-10282-0

Conspicuous and cryptic poison frogs are picky and prefer different meals in syntopy

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Received: 15 June 2023 / Accepted: 24 November 2023

Abstract

The poison frog family (Anura: Dendrobatidae) consists of species with conspicuous (e.g., warning coloration and toxicity or low palatability) and cryptic (e.g., palatable, and inconspicuous coloration) traits. Previous literature suggests that conspicuous, but not cryptic, species require diet specialization in prey high in alkaloids. To test for dietary preferences of poison frog species, we identified, to the lowest possible taxonomic rank, the diets of 21 *Epipedobates darwinwallacei* (conspicuous) and 22 *Hyloxalus awa* (cryptic) frogs living in syntopy in the Otongachi Forest in northwestern Ecuador. We then tested for differences in diet assemblage composition, and diet specialization, in these putatively conspicuous and cryptic frogs. Our analyses showed significant differences in the composition of arthropod assemblages consumed by both frog species, which translated into a narrow niche breadth and nine arthropod taxa (out of a total of 18) consumed by both species. Moreover, the index of relative importance, which measures frog's diet specialization, suggested that *E. darwinwallacei*, and *H. awa* prefer specific arthropod taxa, where the former consumes preferentially springtails and mites, while the latter consumes mostly ants and Coleoptera larvae. Thus, contrary to expectations, diet specialization is not a unique characteristic of the species with conspicuous traits when living in syntopy.

Keywords Niche breadth · Aposematic · Conspicuous · Cryptic · Diet specialization

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Introduction

Trophic ecology of anurans shapes the energy flow of terrestrial and aquatic ecosystems and helps to understand frog assemblage organization, life history, and evolution (Guayara-Barragán 2018; Hughes 2009; Mendoza-Estrada et al. 2008; Stebbins and Cohen 1997). The type of foraging, prey defense mechanism, and microhabitat can shape frog diets (Parmelee 1999). Although various plant and vertebrate groups are part of the anuran food resource, arthropods are essential in frog's diet, with ants and mites being a preferred group in several species (Biavati et al. 2004; Martínez-Coronel and Pérez-Gutiérrez 2011; Moskowitz et al. 2020; Solé and Rödder 2010).

Poison frogs (Anura: Dendrobatidae) include aposematic species, which advertise their toxicity or unpalatability to potential predators with their conspicuous coloration (e.g., species in *Epipedobates* and *Ameerega*; Guillory et al. 2019; Santos et al. 2009). The alkaloids that enable these frogs to effectively communicate their alarm signals are obtained from their prey, such as ants and mites, with high alkaloid contents (Moskowitz et al. 2022; Saporito et al. 2004; Takada et al. 2005). One key characteristic of aposematic dendrobatid frogs is the high degree of diet specialization (Darst et al. 2005; Saporito et al. 2012; Santos et al. 2016; Sanchez et al. 2019). For example, *Oophaga sylvatica, Ameerega hahneli*, and *A. parvula* consume over 80% of ants and mites in their diet *(*McGugan et al. 2016; Darst et al. 2005), *Epipedobates anthonyi* consume 88% of ants and mites, and *A. bilinguis*, approximately 73% of mites and ants (Darst et al. 2005; Santos and Cannatella 2011). Greater alkaloid capture from prey promotes conspicuous colorations, and greater toxicity, by frogs (McGugan et al. 2016; Moskowitz et al. 2018; Saporito et al. 2004, 2012). Because dietary specialization and aposematism have coevolved (Santos et al. 2003), non-toxic species are not expected to specialize in alkaloid-bearing invertebrates like mites and ants, regardless of the composition of the surrounding population (Guayara-Barragán 2018; Konopik et al. 2014). However, this hypothesis has seldom been tested in natural communities.

Not all dendrobatid frogs are aposematic. Species in *Hyloxalus, Nephelobates*, and *Colostethus* (Di Doménico 2016; Grant et al. 2006; Santos et al. 2003) exhibit cryptic coloration that blends with background patterns or colors and is associated with a lack of toxicity and low metabolic rates (Sanchez et al. 2019; Santos and Cannatella 2011). Generalist species consume ants, mites, orthopterans, springtails, and other arthropods to a similar extent (e.g., *Colostethus panamensis*, *C. pratti*, *Hyloxalus maculosus*, and *H. sauli*; Santos and Cannatella 2011; Darst et al. 2005). Without the pressures imposed by aposematism, cryptic species are expected to be opportunistic and consume a variety of prey (Hothem et al. 2009; Silva et al. 2009), which could result in generalist diets with high mobility and solitary habits (Coloma 1995; Luría-Manzano et al. 2019; Santos et al. 2003). Nonetheless, prey selection and feeding behavior of cryptic species are expected to be shaped by general optimal foraging expectations on frog and prey morphology (Parmelee 1999; McElroy and Donoso 2019). For example, larger frogs consume more and larger prey (Guzmán and Salazar 2012; Blanco 2016), and the physical characteristics of prey, such as color, body size, and hairiness, influence their predation rates (McElroy and Donoso 2019).

Maybe because of their conspicuousness, previous studies have focused on aposematic species and their ability to sequester alkaloids, while diets of cryptic species have been poorly documented (Darst et al. 2005; Velasco 2018; Klonoski et al. 2019; Ledón-Rettig et al. 2010; Moskowitz et al. 2022; Nadaline et al. 2019; Santos et al. 2016; Saporito et al. 2007). Small prey (e.g., ants, termites, and mites) provide high nutritional value and alkaloids that are sequestered by aposematic frogs (Moskowitz et al. 2018, 2020; Parmelee 1999). Moreover, prey items in diets usually come from leaf litter, as insects in topsoil provide greater amounts of alkaloids to aposematic frogs than other insects from different substrates (Daly et al. 1994). Here, for the first time, we study the diets of two frog species living in syntopy (i.e., coexisting in the same microhabitat, Gagliardi-Alvarez 2019): *Epipedobates darwinwallacei*, with conspicuous (putatively aposematic) coloration, and *Hyloxalus awa*, with cryptic coloration), focusing on its composition and degree of specialization.

Methods

Collection of anurans and prey identification

We conducted this study at the Otongachi Forest, located at 00°08’49”S and 78°57’15”W, 850 m asl, in Pichincha Province in the Western Cordillera of the Andes in Ecuador (Donoso and Ramón 2009). The Otongachi forest is a 20-ha patch of the Otonga Integral Forest (BIO Reserve), located at the edge of Unión del Toachi River (Arcos-Argoti 2011), with 1000–2000 mm of annual rainfall and a mean temperature of 18 to 24 °C (Cañadas 1983; Donoso 2017). We collected samples in areas where populations of *Epipedobates darwinwallacei* and *Hyloxalus awa* are found in syntopy (Angulo et al. 2006). Because these are diurnal species (Grant et al. 2006), the sampling effort was in daylight hours between 05:30 and 13:30, and between 14:30 and 19:00 h for seven days in May and July 2021. Six individuals per frog species were kept as vouchers and deposited at the Museum of Zoology at Universidad Tecnológica Indoamérica (MZUTI, *Epipedobates darwinwallacei*: ZC-0525-6, ZC-0528-9, ZC-0530-1; *Hyloxalus awa*: ZC-0521-4, ZC-0527, ZC-0532). We only collected data from adults and subadults, with a snout-vent length (SVL) greater than 13.5 mm for *Epipedobates darwinwallacei*; and greater than 15.0 mm for *Hyloxalus awa* (Martínez-Coronel and Pérez-Gutiérrez 2011; Ramírez-Valverde et al. 2020; Páez-Vacas et al. 2010).

We extracted diets from frog stomachs with the washing technique described by Solé et al. (2005) within two hours of capture. Briefly, we collected 20 ml of water from the stream where the individual was collected with a sterile syringe and a 2 mm diameter silicone tube. We opened the snout to carefully introduce the tube through the esophagus until it reached the stomach. The stomach content or reflux obtained was washed and preserved in 70% ethanol. We identified prey down to the lowest possible taxonomic category (Order of Family), and for Coleoptera, we recorded adults and larvae. We measured prey items on photographs taken with an SC30 digital camera and Olympus Stream V.2.3.3 image analysis software mounted in an Olympus SZ61 stereomicroscope.

Diet analysis

All analyses were done in R v.4.1.2 (R Core Team 2021). First, we tested if there was a general relationship between the volume of stomach contents (V) and frog morphology (snout-vent length, SVL and snout width, SW), with a Pearson correlation. Prey volume determines the amount and size of prey that can be consumed by each frog species (Guzmán and Salazar 2012; Menéndez-Guerrero 2001). For this, we used the formula: $V = (4\pi/3) *$

(Length/2) * (Width/2)^2, where the width of the prey corresponds to the middle part of the body, without counting the appendages, and the length is measured from the tip of the head to most distal body part (Moskowitz et al. 2020). The normality of the data was determined with a Shapiro-Wilk test (Luría-Manzano et al. 2019). Non-normal data were transformed with a natural logarithm. For interpretation, values of r equal to or smaller than 0.35 are considered no or low correlation, between 0.36 and 0.67 modest or moderate correlation, and 0.68 to 1 strong or high correlation (Taylor 1990).

To test for differences in arthropod assemblage composition between species, we performed an analysis of similarity (ANOSIM; Oksanen et al. 2020) on volume and abundance matrices. ANOSIM provides an R-index with values between -1 and 1. R values close to 1 suggest dissimilarity between groups, and values close to –1 indicate similarity. Significance was assessed with a $p<0.05$ (Chapman and Underwood 1999). We calculated the dissimilarity matrix with the Bray-Curtis distance. We then used a non-metric multidimensional scaling (NMDS) to visualize prey assemblages of frog species in a two-dimension plot (Moskowitz et al. 2020; Saporito et al. 2012). For this, we used only prey categories sampled in more than one frog stomach. An NMDS provides a Stress value that ranges from 0 to 1. Stress values <0.2 suggest that distances in the plot are good representations of distances in the assemblage matrix. We perform these analyses with the *vegan* package (Oksanen et al. 2020) in R. To analyze the overlap in the diet of both frogs, we applied the trophic niche overlap index: $O_{jk}=O_{kj}=\Sigma\ (P_{ij}\ xP_{ik})/\surd(\Sigma P_{ij}\hat{}2\ x\Sigma P_{ik}\hat{}2\ )$ (Pianka 1973) in the R package *Biodiversity R* (Kindt and Coe 2005). Here, P_{ij} and P_{ik} determine the proportions of prey used by each species (“*j*” and “*k*”). The analysis provides a symmetrical index between 0 (non-overlap) and 1 (overlap) (Gambale et al. 2020).

To assess the representativeness of the food categories in frog stomachs, we calculated a hierarchy index (*HI*). To calculate *HI*, the highest value of the *IRI* is taken as the reference, and percentage values are assigned to the remaining taxa (Aun and Martori 1998; González et al. 2012; Villavicencio et al. 2005). Here, a taxon is considered ‘fundamental’ if it has a *HI* between 100% and 75%, ‘secondary’ for values at 75–50%, ‘accessory’ with 50–25%, and ‘incidental’ for values below 25% (Aun and Martori 1998; González et al. 2012; Mina-Angulo et al. 2019). *HI* uses an index of relative importance (*IRI*; Pinkas et al. 1971) to determine the hierarchy of arthropod taxa consumed. The *IRI* is an index that helps describe the importance of each arthropod taxa consumed in the diets of the two frogs (Biavati et al. 2004; Valderrama-Vernaza et al. 2009). To calculate *IRI*, we used the formula, $IRI=\%FO*(\%N+\%V)$, where: $\%FO$ represents the relative frequency of occurrence of a food category in stomachs; $\%N$ represents the relative abundance of each prey category in the diet; and $\%V$ expresses the relative volumetric of the prey in the diet (nutrient contribution of individual prey) (Pinkas et al. 1971). Therefore, *IRI* reduces biases caused by either small prey in large numbers or a few relatively large prey (Aun et al. 1999).

To determine the significance of trophic niche breadth and level of specialization, we applied the standardized Levin’s index, $B_{sta}=(B–1)/(n–1)$, where n is the number of items recorded, B corresponds to $B=1/\sum (P_i^2)$, P is the proportion of each resource category and i is the prey category (Krebs 1999; Moser et al. 2017). Here, B_{sta} is expressed between 0 (narrow niche) and 1 (broad niche). Values below 0.5 are considered specialists (Sanches et al. 2019). Specialization of a frog species is indicated by a proportional value of any taxa in its diet with *HI* greater than 70% and a niche breadth (B_{sta}) less than or equal to 0.5 (Sanches et al. 2019; Santos and Cannatella 2011).

Results

We captured 21 individuals of *Epipedobates darwinwallacei*: 20 adults and one subadult with diet in the stomachs (SVL=17.33±1.71 mm; SW=5.34±0.46 mm). Some additional eight specimens (seven adults and one subadult) were found with an empty stomach and were thus not included in our analysis. For *Hyloxalus awa*, we found 22 individuals: 20 adults and two subadults (SVL=20.57±2.39 mm; SW=6.83±1.18 mm), we also captured four juvenile specimens. Excluding frogs with empty stomachs and juveniles, we studied 21 individuals of *E. darwinwallacei* and 22 individuals of *H. awa*. For *E. darwinwallacei*, we identified 61 prey items classified into 13 arthropod taxa (mean=2.90±3.62 items per stomach). For *H. awa*, we found 108 prey items categorized into 14 arthropod taxa (mean=4.91±2.79). In total, we found 18 arthropod taxa in both frogs, and nine of these arthropods are shared by *E. darwinwallacei* and *H. awa*. Additionally, the stomach contents volume (V) of *E. darwinwallacei* was V=0.49±0.50 mm^3, and of *H. awa*, V=14.15±24.60 mm^3. There was no correlation between SVL and SW with V of the two species (*E. darwinwallacei*: $r = -0.08$ for SVL, and $r = -0.22$ for SW; *H. awa*: $r = 0.03$ for SVL, and r=0.33 for SW).

The NMDS showed a slight overlap in the diets of both species, however, ANOSIM corroborated significant differences in the diet composition of the frog species for abundance ($r = 0.33$, $p = 0.001$), and volume ($r = 0.29$, $p = 0.001$) data (Fig. 1). We found that approximately half of the prey present in the stomachs are shared between *E. darwinwallacei* and *H. awa* (Ojk=0.48). The importance relative index (*IRI*) of arthropod taxa in *E. darwinwallacei* shows that Collembola (*IRI*=2446.9) and Acari (*IRI*=2415.2) were the most important resources, found in 10 and 12 stomachs, respectively (Table 1). In *H. awa*, Hymenoptera (Formicidae; *IRI*=2162.4) is the main resource used, followed by Coleoptera larvae (*IRI*=2102.5), found in 14 and 10 stomachs, respectively. Both species show a narrow trophic niche breadth ($B_{sta} < 0.5$). *Epipedobates darwinwallacei* is specialized ($B_{sta} = 0.22$) in the consumption of Collembola (*HI*=100%) and Acari (*HI*=99%), classified as a "fundamental" resource in its diet because percentages are between 75 and 100%. *Hyloxalus awa* is slightly less specialized ($B_{sta} = 0.28$), with a diet based on Formicidae

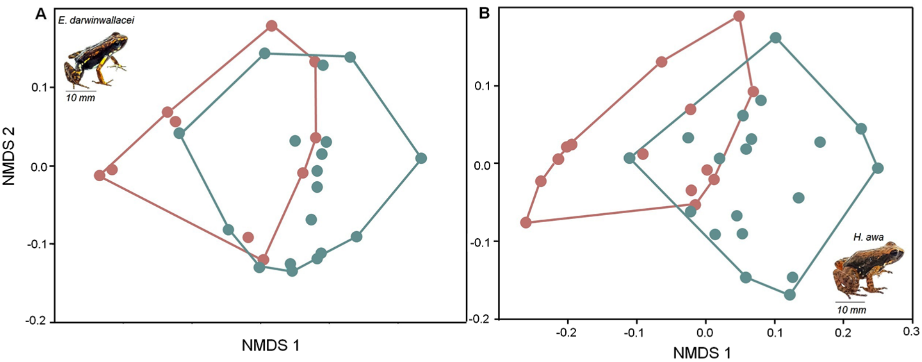

Fig. 1 Non-metric multidimensional scaling (NMDS) analysis based on Bray-Curtis dissimilarity shows the difference of (**A**) the abundance of prey consumed by *Epipedobates darwinwallacei* and *Hyloxalus awa* (*Stress: 0.22*), and (**B**) volume of prey consumption between *E. darwinwallacei* and *H. awa* (*Stress: 0.23*). Each point represents the diet of each frog studied (pink for *E. darwinwallacei*, and turquoise for *H. awa*)

Table 1 Relative importance (*IRI*) and hierarchical index (*HI*) of arthropod taxa from stomach contents of *Epipedobates darwinwallacei* and *Hyloxalus awa*. N = number of prey; V = volume of stomachs; O = occurrence of prey in stomachs; *IRI* = Relative Importance Index; *HI* = Hierarchy Index

Item	*E. darwinwallacei* (B_{sta} = 0.22)**					*H. awa* (B_{sta} = 0.28)**				
	N	V	O	*IRI*	HI (%)	N	V	O	*IRI*	HI (%)
Acari	**21**	**0.81**	**12**	**2415.2**	**99***	5	1.2	3	68.5	3.2
Arachnida	-	-	-	-	-	2	23	2	82.9	3.8
Coleoptera	2	0.29	2	57.9	2.4	6	45	4	363.8	17
Collembola	**12**	**3.28**	**10**	**2446.9**	**100***	15	5.7	12	856.7	40
Dermaptera	2	0.20	2	49.4	2	-	-	-	-	-
Diptera	3	0.99	3	207.5	8.5	11	6.5	10	558.5	26
Hemiptera	-	-	-	-	-	12	5	9	520.3	24
Formicidae	3	0.50	3	139.1	5.7	**31**	**16**	**14**	**2162.4**	**100***
Other Hymenoptera	-	-	-	-	-	3	2.7	3	49.5	2.3
Isopoda	1	0.34	1	23.7	1	5	83	5	710.0	33
Ixodidae	-	-	-	-	-	2	1.7	2	21.9	1
Larv. Coleoptera	8	2.64	5	919.9	38	**11**	**112**	**10**	**2102.5**	**97***
Mollusca	-	-	-	-	-	3	8.4	3	74.8	3.5
Oribatida	4	0.18	2	79.1	3.2	1	0.2	1	4.5	0.2
Plecoptera	1	0.69	1	39.4	1.6	1	0.7	1	5.2	0.2
Protura	1	0.17	1	15.4	0.6	-	-	-	-	-
Psocoptera	2	0.20	2	49.6	2	-	-	-	-	-
Siphonaptera	1	0.06	1	10.4	0.4	-	-	-	-	-

*Bold values of the hierarchy index (*HI* > 70%) indicates preference for taxa in the prey. **Specialization was determined by combining B_{sta} (< 0.5) and *HI*.

(HI = 100%) and Coleoptera larvae (HI = 97%), and these are also "fundamental" resources in its diet. Additionally, Acari and Collembola are consumed by *H. awa*, as are Formicidae, and beetle larvae are preyed upon by *E. darwinwallacei*, but in minimal quantities (< 40%, "accessory" or "incidental"). Other prey eaten by both species include Diptera, Coleoptera, Isopoda, Oribatida, and Plecoptera (< 25%, "incidental").

Discussion

Both the putatively aposematic frog *Epipedobates darwinwallacei* and the cryptic frog *Hyloxalus awa* showed specialization in their diet when living in syntopy. *Epipedobates darwinwallacei* specialized in consuming Acari and Collembola; and *H. awa* preferred ants and Coleoptera larvae. Moreover, Dermaptera, Protura, Psocoptera, and Siphonaptera were exclusive to *E. darwinwallacei*; and, Arachnida, Hemiptera, Hymenoptera (non-ants), and Mollusca were exclusive to *H. awa*. The composition of the diets of *Epipedobates darwinwallacei* and *Hyloxalus awa* were significantly different despite an overlap of about 50% of prey items consumed, suggesting there is no overlap in the trophic niches of the two species. Previous studies in anurans show that trophic niches do not overlap in syntopy and genetically close species because they divide resources, which favors coexistence and reduces competition (Avellaneda-Moreno 2016; Muñoz-Guerrero et al. 2007; Oliveira et al. 2015; Palacio-Núñez et al. 2008; Paucar Guerra 2013). An example is Collembola, which is known for its high abundance in the leaf litter layer of tropical forests and found in the diet of both dendrobatid frogs (Dietl et al. 2009; Fittkau and Klinge 1973; Noll et al. 2018). Nonetheless, Collembola was important for *E. darwinwallacei*, but not for *H. awa*. Therefore, our results suggest that by focusing on different preys, *E. darwinwallacei* and *H. awa* coexist in syntopy.

While this is the first study to report the diet of *E. darwinwallacei*, others have found *Epipedobates* species to be specialists in relatively small prey. *Epipedobates anthonyi* (N = 10) in Cuenca (Ecuador) has a 90% ant-based diet (Darst et al. 2005; Santos and Cannatella 2011). *Epipedobates boulengeri* (N = 32) in Imbabura (Ecuador) consume larger numbers of mites and springtails than any other prey (27% and 31%, respectively; Caldwell 1996; Santos and Cannatella 2011). To our knowledge, this is the first study that reports Dermaptera, Protura, Psocoptera, and Siphonaptera in the diet of *Epipedobates.* Moreover, in *E. darwinwallacei*, mite specialization might contribute to aposematism, as mites are an important source of alkaloids for poison frogs (McGugan et al. 2016; Moskowitz et al. 2020; Saporito et al. 2012, 2015).

We found that *Hyloxalus awa* also prefers ants. The ant genera most frequently consumed were *Anochetus*, *Solenopsis*, and *Azteca*. These ants have a high alkaloid content and belong to the subfamilies Formicinae and Myrmicinae, which are usually selected by toxic dendrobatid frogs (Clark et al. 2005; Moskowitz et al. 2022; Prates et al. 2019; Santos et al. 2016). Some species of the genus *Hyloxalus* feed on ants at a high percentage compared to other prey, but they are not considered specialists on these prey (e.g., *H. maculosus*, 22% and *H. sauli*, 60%; Santos and Cannatella 2011; Darst et al. 2005). Other species of *Hyloxalus* have been described as diet generalists, consuming several species of leaf litter arthropods (e.g., *H. yasuni*; Menéndez-Guerrero 2001; Paucar Guerra 2013). In our study site, ant communities have not undergone temporal structural change, even if there are annual rotations at the species level (Donoso 2017). However, the sample size, seasonality, and multiyear variability in arthropod communities may influence variation in prey abundance, consumption volume, and the presence of new prey in frog stomachs (Aun et al. 1999; Donoso 2017; Nieva Cocilio 2019). As these variables and temporal changes could affect niche width and diet overlap (da Rosa et al. 2006; Moser et al. 2017; Gambale et al. 2020), assessing the diets of *H. awa* through time will help us identify whether, despite these year-to-year changes in ant species, *H. awa* continues to prefer ants in its diet.

In contrast to previous research (Santos and Cannatella 2011; Darst et al. 2005), we found both the putatively aposematic and the cryptic species to be specialized predators. Examples of aposematic frogs with narrow trophic niches and a specialist diet are *Ameerega bilinguis*, *A. hahneli*, *A. parvula*, *Allobates insperatus* (Darst et al. 2005), *Dendrobates auratus* (Caldwell 1996) and *Oophaga pumilio* (Caldwell 1996; Moskowitz et al. 2018, 2020). However, not all *Epipedobates* are diet specialists, for instance, *Epipedobates boulengeri* exhibits broad trophic niche breadth, consumption of diverse prey (generalist), and cryptic coloration (Cadwell 1996). On the other hand, species with cryptic coloration, such as *Allobates zaparo*, *A. femoralis*, *A. talamancae* (Grant et al. 2017; Darst et al. 2005), *Hyloxalus bocagei* (Menéndez-Guerrero 2001) and *Silverstoneia nubicola* (Toft 1981) usually show wide trophic niches. However, there are some cryptic frogs, such as *Hyloxalus sauli*, which show specialized diets, which translates to narrow trophic niches and (at least in this case) preference for ants (Cadwell 1996; Darst et al. 2005; Santos and Cannatella 2011). In addition, *H. nexipus* and *H. azureiventris* show aposematic colorations and possess skin alkaloids, but their diet has not yet been characterized (Santos and Cannatella 2011).

Frog body and mouth size are critical for prey consumption (Luría-Manzano 2012; Nieva-Cocilio 2019; Parmelee 1999). Both frog species studied here were found to consume relatively small prey items, which is common for dendrobatid species (Parmelee 1999; Saporito et al. 2007; Moskowitz et al. 2018, 2020). Some dendrobatid frog species (e.g., *Epipedobates bilinguis*, *Colostethus* sp., *Hyloxalus sauli*) present positive correlations between body and prey size (Menéndez-Guerrero 2001). In addition, correlations between frog body and prey size are positive in the leaf litter anurans in Panama and Peru (Toft 1981). However, we did not find a correlation between frog body size and prey size in the two species, which agrees with other studies on dendrobatids, as in *Phyllobates aurotaenia* and *Dendrobates truncatus* (Marín-Martínez et al. 2019; Mina-Angulo et al. 2019). Thus, our result contrasts with other studies which found positive correlations between morphology (SVL and SW) and the volume of prey consumed in anurans (Guzmán and Salazar 2012; Luría-Manzano et al. 2019; Nieva-Cocilio 2019).

In our study, even though we considered *E. darwinwallacei* and *H. awa* to be conspicuous and cryptic, respectively, we acknowledge that experimental evidence that *E. darwinwallacei* is aposematic is lacking (Cisneros-Heredia and Yánez-Muñoz 2010; Coloma 1995). Although it is well-known that dendrobatids frogs are often brightly colored, and colors serve as a defensive function to warn predators of defensive alkaloids (Santos et al. 2003), there is also evidence that colors may serve other purposes (Maan and Cummings 2012; Lawrence et al. 2019). For example, some species may be cryptic at long range and display warning textures and colors at close range (Barnett et al. 2018). Also, the light environment can alter and influence frog color patterns and affect detectability from predators (Rojas et al. 2014). Additionally, some species use colors as sexual signals (Maan and Cummings 2008). Similarly, there are species in *Hyloxalus*, a genus typically considered cryptic, that have conspicuous traits (e.g., *H. nexipus*) and alkaloid reserves (e.g., *H. azureiventris*; Santos and Cannatella 2011). Therefore, exploring the factors influencing color variation will advance our understanding of the relationship between color variation, aposematism, and diet specialization.

Overall, we found that both *Epipedobates darwinwallacei* (putatively aposematic) and *Hyloxalus awa* (cryptic) have preferences/specializations in their diets, contradicting the prediction that cryptic species are generalists. Although they live in syntopy, the two frog species do not overlap in their trophic niche. *Epipedobates darwinwallacei* and *H. awa* are specialized in prey that may contain alkaloids (mites and ants, respectively) (Saporito et al. 2004, 2015). We suggest that to understand the role of food specialization in aposematic and cryptic species, species should be studied in syntopy to determine if competition for specific prey and prey partitioning affects food specialization.

Acknowledgements We thank the Ministry of Environment and Water of Ecuador, for the approval of the collection and research protocols (MAAE-ARSFC-2021-1219). The Applied Biology Laboratory of the Faculty of Agronomy, directed by Aníbal Pozo of the Central University of Ecuador, provided infrastructure and equipment for diet analysis of the two frog species. We thank Gabriela Maldonado and Nicolás Del Castillo for their dedication and hard work in logistical support during fieldwork, and Diego Domínguez for his extensive knowledge and support in identifying arthropod taxa. This work was submitted in partial fulfillment of SS's Master degree at Universidad Tecnológica Indoamérica. Sofía Carvajal-Endara and Andrea Terán-Valdés served as examining board in the oral defense and provided valuable feedback. DAD thanks Escuela Politécnica Nacional for a Licencia to conduct postdoctoral research. MIP thanks Jeffrey L. Coleman for discussions on aposematism in poison frogs. Finally, we thank two anonymous reviewers for valuable feedback on earlier versions of this manuscript.

Author Contributions All authors conceived the ideas and designed the study; SS collected and analyzed data. SS and MIP wrote the initial draft of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Funding (information that explains whether and by whom the research was supported):
This study was supported by Universidad Tecnológica Indoamérica (UTI, Quito-Ecuador).

Data Availability Data will be available upon publication of the manuscript.

Code Availability Not applicable.

Declarations

Ethics approval The Ministry of Environment and Water of Ecuador approved the collection and experimental protocols (MAAE-ARSFC-2021-1219).

Consent to participate Not applicable.

Consent for publication Not applicable.

Competing interests The authors declare no competing interests.

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