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Diet of *Engystomops pustulosus* (Anura: Leptodactylidae) from Colombia and current knowledge of its dietary ecology

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Abstract

Diet of *Engystomops pustulosus* (Anura: Leptodactylidae) from Colombia and current knowledge of its dietary ecology. We investigated the diet of *Engystomops pustulosus* from a population in the Middle Magdalena River valley, including an evaluation of the effect of body and head size on prey number and volume. We present the current state of knowledge of the diet of *E. pustulosus* from published information in addition to our data. We found a total of 400 prey items representing two phyla, Arthropoda and Mollusca; seven orders and nine families were detected. Arthropods, mainly insects, were the most frequent prey in the diet. Among arthropods, Acari and Isoptera were numerically dominant. We did not observe effects of body and head size on prey number and volume. The published literature of the diet of *E. pustulosus* included 66 prey items, among which Isoptera (termites), Acari, and Formicidae were the most common groups, suggesting dietary specialization. Prey items consumed by *E. pustulosus* varied among different localities; Blattodea, Orthoptera, and Thysanoptera were unique at certain localities. Further study of prey availability and diets associated with land-use changes across major geographic localities will contribute to a better understanding of the predator-prey interactions in these anthropogenic environments.

Keywords: Ecosystem, Feeding habits, Frog, Predator interaction, Trophic specialist.

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Resumen

Dieta de *Engystomops pustulosus* (Anura: Leptodactylidae) de Colombia y conocimiento actual de su ecología alimentaria. Investigamos la dieta de *Engystomops pustulosus* de una población del valle medio del río Magdalena, incluyendo una evaluación del efecto del tamaño del cuerpo y de la cabeza sobre el número y volumen de presas. Presentamos el estado actual de conocimiento sobre la dieta de *E. pustulosus* a partir de información publicada más nuestros datos. Encontramos un total de 400 presas representando dos phyla, Arthropoda y Mollusca; siete órdenes y nueve familias de invertebrados. Los artrópodos, principalmente insectos, fueron las presas más frecuentes en la dieta. Entre los artrópodos, Acari e Isoptera fueron numéricamente dominantes. No se observaron efectos del tamaño del cuerpo y la cabeza sobre el número y volumen de presas. La literatura publicada sobre la dieta de *E. pustulosus* incluyó 66 taxones presas, entre los que Isoptera, Acari y Formicidae fueron los grupos más comunes, lo que sugiere una especialización en la dieta. Las presas consumidas por *E. pustulosus* varían entre localidades; Blattodea, Orthoptera y Thysanoptera, son únicos en algunas localidades. Estudios más detallados de la disponibilidad de presas y dietas asociadas a los cambios en el uso del suelo en mas localidades geográficas contribuirá a una mejor comprensión de las interacciones depredador-presa en estos entornos antropogénicos.

Palabras clave: Ecosistema, Especialización trófica, Hábitos alimentarios, Interacción depredadora, Rana.

Resumo

Dieta de *Engystomops pustulosus* (Anura: Leptodactylidae) da Colômbia e conhecimento atual de sua ecologia alimentar. Investigamos a dieta de *Engystomops pustulosus* de uma população do vale médio do rio Magdalena, incluindo uma avaliação do efeito do tamanho do corpo e da cabeça sobre o número e o volume das presas. Apresentamos o estado atual do conhecimento sobre a dieta de *E. pustulosus* com base em informações publicadas e em nossos próprios dados. Encontramos um total de 400 itens alimentares representando os filos Arthropoda e Mollusca; sete ordens e nove famílias de invertebrados. Artrópodes, principalmente insetos, foram os itens mais frequentes na dieta. Entre os artrópodes, Acari e Isoptera foram numericamente dominantes. Não foram observados efeitos do tamanho do corpo e da cabeça sobre o número e o volume de presas. A literatura publicada sobre a dieta de *E. pustulosus* incluiu 66 táxons, entre os quais Isoptera, Acari e Formicidae foram os grupos mais comuns, sugerindo especialização na dieta. Os itens consumidos variaram entre as localidades; Blattodea, Orthoptera e Thysanoptera foram exclusivos de algumas localidades. Estudos mais detalhados da disponibilidade de presas e dietas associadas a mudanças no uso do solo em mais localidades geográficas contribuirão para uma melhor compreensão das interações predador-presa nesses ambientes antropogênicos.

Palavras-chave: Ecossistema, Especialização trófica, Hábitos alimentares, Interações predador-presa, Rã.

Introduction

Understanding trophic interactions is essential to disentangling community assembly processes and ecosystem functioning (Ings *et al.* 2009, Ryser *et al.* 2021). The study of trophic interactions has traditionally focused on the use of species diet proxies (Morales-Castilla *et al.* 2015, Laigle *et al.* 2018), primarily because diet preferences affect ecosystem energy flow and influence inter- and intraspecific interactions (Cloyed and Eason 2017). Anurans are a key vertebrate group used to study trophic interactions given their role in ecosystem energy transformation (Colón-Gaud *et al.* 2009) and the high consumption of invertebrates (Solé and Rödder 2010, Vitt and Caldwell 2014). As such, the study of diet in these vertebrates is essential to understanding ecosystem functioning and stability (Connelly *et al.* 2008, Whiles *et al.* 2013).

Anuran diet composition may vary across space (Maneyro and da Rosa 2004, Miranda *et al.* 2006), time, and species functional traits (Vitt and Caldwell 2014, Atencia *et al.* 2020). Spatial conditions, for instance, have strong effects on the abundance and diversity of invertebrates (e.g., Eisenhauer *et al.* 2011, López-Bedoya *et al.* 2021, 2022a). These changes among invertebrate communities may in turn impact prey composition of anurans (Agudelo-Cantero *et al.* 2015, Moroti *et al.* 2021). Likewise, functional traits such as body size (snout–vent length; SVL) or mouth morphology (mouth width; MW) act as limiting factors on the size of prey that anurans can ingest, thus affecting prey composition (Parmelee 1999, Moroti *et al.* 2021).

Engystomops pustulosus (Cope, 1864) is a species widely distributed in lowlands (0-1300 m) in northern South America (Colombia, Guyana and Venezuela; Köhler 2011, Cole *et al.* 2013, Ospina-L and Bedoya-Cañón 2018, Barrio-Amorós *et al.* 2019). Despite its relatively wide geographic distribution, its diet has been rarely studied except in a few localities from Colombia and Venezuela (e.g., González-Duran *et al.* 2012, Viña-Albornoz *et al.* 2020, Blanco-Torres *et al.* 2021a). The main goals of our study are threefold: (i) to describe diet composition of a previously studied Colombian population; (ii) to test the relationship between snout-vent length (SVL) and maximum width of the mouth (MW) and prey number and prey volume; and (iii) to examine the current state of knowledge of the diet of *E. pustulosus* considering all extant information.

Materials and Methods

Study Area

The study area was the San Pedro farm (5.559946, -74.860329; 470 m a.s.l.; municipality of Victoria, Caldas department, Colombia). The San Pedro farm is located in the Middle Magdalena River valley, an area with a mean precipitation of 5500 mm/year, distributed in two rainy seasons (April–May and September–December), with an average temperature of 25°C (Cardona *et al.* 2010). The landscape consists of degraded primary forest, cattle pastures, and cocoa or annual crop plantations.

Sampling Design and Laboratory Work

We sampled the population of *E. pustulosus* using visual encounter surveys (see Doan 2003) in ponds associated with cattle pastures for three consecutive days (19–21 April 2016), between 18:00 and 23:00 h. We captured frogs manually and transferred them to the field station within a maximum of two hours after capture to minimize bias associated with digestion (Parmelee 1999). The frogs were sacrificed using Xylocaine and fixed in 10% formaldehyde (Gutierrez-Cárdenas *et al.* 2016). Snout–vent length (SVL) and mouth width (MW) were measured for each specimen with a digital caliper to the nearest 0.1 mm. Specimens were preserved in 75% ethanol and transported to the zoology laboratory of the Universidad de Caldas.

Stomach contents were identified for each individual using a stereomicroscope; small prey such as Acari and Formicidae were identified using a microscope. We identified prey to the lowest possible taxonomic level using general keys for invertebrates (Triplehorn and Johnson 2005, Adis 2002) and specific keys for Coleoptera (Arnett Jr. and Thomas 2000), Hymenoptera (Fernández 2003, Fernández *et al.* 2015, Ješovnik and Schultz 2017, Fernández *et al.* 2019, Pérez-Pedraza and Fernández 2019), and Acari (Balogh and Balogh 1988, 1990, Badejo 2002).

Stomach Contents Analysis

Prey consumption of *E. pustulosus* was quantified as the number of prey items (N_i), volume of prey items (V_i), and frequency of occurrence (O_i) of each prey taxon (*see*

Gutiérrez-Cárdenas *et al.* 2016). Each individual prey item was measured for length (L) and width (W) using a stereomicroscope coupled with digital measuring to the nearest 0.1 mm. These measurements were employed to estimate the prey volume (mm^3) using the formula for a prolate spheroid [$V_i = 4/3\pi\ (L/2)\ (W/2)^2$] (Dunham 1983).

We compared the relative proportion of each prey category using the index of relative importance (IRI) following Pinkas *et al.* (1971): $\%IRI = (\%O_i)\ (\%N_i + \%V_i)$. The latter was done because any measurements used alone are biased toward large-sized or sporadically abundant prey (Pinkas *et al.* 1971, Manicom and Schwarzkopf 2011). Finally, we evaluated the correlation between functional traits and prey of *E. pustulosus*. We tested for correlations between SVL and MW to prey number and prey volume using the Spearman Rank Correlation (r_s) on log-transformed data in the R program (R Core Team 2022).

Current State of Knowledge of the Diet of E. pustulosus

To describe the diet of *E. pustulosus*, we included published articles from the personal database of the last author (PDAGC), in addition to articles identified in the recent revision of the Neotropical herpetofauna (*see* Urbina-Cardona *et al.* 2023). When multiple studies were published from the same dietary dataset (e.g., Blanco-Torres *et al.* 2020, 2021a, b), we included only one study to avoid duplication of data (i.e., the study showing more detailed information). For each study we extracted the following variables: (i) country, (ii) year of publication, (iii) habitat cover, and (iv) prey items consumed by *E. pustulosus*.

Results

We captured 58 individuals of *E. pustulosus* [52 males and six females; mean SVL, 27.4 ± 1.59 mm (range 24.37–30.94 mm); MW of 7.56 ± 0.63 mm (6.25–8.87 mm)]. We used only the 63.8% (N = 37) of individuals that contained prey items.

A total of 400 prey items were distributed in two phyla, Arthropoda and Mollusca, which included seven orders and nine families, primarily insects (Table 1). Acari (mites; $\%N_i$ = 48.75) and Isoptera (termites; $\%N_i$ = 41) were the numerically dominant prey taxa. Volumetrically, Isoptera ($\%V_i$ = 86.2) and Formicidae ($\%V_i$ = 6.49) were the dominant prey items. Isoptera ($\%O_i$ = 51.35) and Formicidae (ants; $\%O_i$ = 45.95) were the most frequently consumed prey items. Isoptera (IRI = 3009.67) and Acari (IRI = 1394.44) were the taxa with the highest IRI values in the diet of *E. pustulosus*. We did not find significant correlations between prey number (r_s = -0.035, p = 0.838; N = 37) and prey volume (r_s = 0.032, p = 0.852; N = 37) with SVL. Likewise, no correlations were found for prey number (r_s = 0.202, p = 0.230; N = 37) and prey volume (r_s = 0.030, p = 0.857; N = 37) with MW.

Seven studies of the diet of *E. pustulosus* includes our present work (Table 2). These studies were made during the last two decades and have focused on the composition of prey assemblages consumed by the species in cattle pastures. Among these studies, 66 prey items were consumed by *E. pustulosus,* with Isoptera, Formicidae, and Acari as the dominant prey taxa in terms of prey number (Table 3). Different prey items occurred in the stomach contents among geographic localities: some invertebrate prey items were unique to a single geographic locality. For example, Blattodea (cockroaches) was found only in stomach contents in a locality from Venezuela, and other prey items such as Collembola, Coleoptera, Diptera, Hemiptera, and Orthoptera were found in other geographic localities (Table 3).

Discussion

We investigated the diet composition of a previously studied Colombian population of *E.*

Table 1. Prey composition of the diet of *Engystomops pustulosus* from Victoria municipality (Caldas, Colombia). Abbreviations: *N*, number of prey items; V, prey volume (in mm^3); O, frequency of occurrence; IRI, index of relative importance (only for prey taxa in which it was possible to calculate the volume).

Prey taxa	*N* (%)	V (%)	O (%)	IRI
ARTHROPODA				
Arachnida				
Araneae	1 (0.25)	0.52 (0.04)	1 (2.70)	0.77
Acari (Oribatida)				
Ceratozetidae	2 (0.50)	0.66 (0.04)	2 (5.41)	2.94
Trhypochthoniidae				
Archegozetes sp.	193 (48.25)	47.78 (3.24)	10 (27.03)	1391.5
Diplopoda				
Polydesmida				
Fuhrmanodesmidae				
Fuhrmannodesmus sp.	1 (0.25)	1.57 (0.11)	1 (2.70)	0.96
Insecta				
Coleoptera				
Chrysomelidae	1 (0.25)	10.47 (0.71)	1 (2.70)	2.59
Staphylinidae				
Paederinae	1 (0.25)	18.85 (1.28)	1 (2.70)	4.13
Euconnus sp.	3 (0.75)	17.28 (1.17)	2 (5.41)	10.38
Hymenoptera				
Figitidae	1 (0.25)	2.36 (0.16)	1 (2.70)	1.11
Formicidae				
Myrmicinae	6 (1.50)	46.29 (3.13)	5 (13.51)	62.63
Atta cephalotes	1 (0.25)	1.18 (0.08)	1 (2.70)	0.89
Cyphomyrmex sp.	2 (0.50)	2.82 (0.19)	1 (2.70)	1.87
Myrmicocrypta sp.	1 (0.25)	1.05 (0.07)	1 (2.70)	0.87
Pheidole sp. 1	8 (2.00)	6.28 (0.43)	3 (8.11)	19.67
Pheidole sp. 2	6 (1.50)	14.66 (0.99)	2 (5.41)	13.47
Sericomyrmex amabilis	3 (0.75)	10.60 (0.72)	1 (2.70)	3.97
Solenopsis sp.	1 (0.25)	3.53 (0.24)	1 (2.70)	1.32
Strumigenys grytava	1 (0.25)	0.52 (0.04)	1 (2.70)	0.77
Strumigenys marginiventris	1 (0.25)	7.33 (0.50)	1 (2.70)	2.02
Wasmannia auropunctata	2 (0.50)	1.77 (0.12)	2 (5.41)	3.35
Isoptera				
Kalotermitidae	71 (17.75)	1144.33 (77.48)	8 (21.62)	2059.11
Termitidae	93 (23.25)	128.83 (8.72)	11 (29.73)	950.56
MOLLUSCA				
Pulmonata	1 (0.25)	8.38 (0.57)	1 (2.70)	2.21
TOTAL	**400**	**1476.86**		

Table 2. Literature on the diet of *Engystomops pustulosus*. Details on country, publication year, habitat cover, study type, taxonomy of prey items, and relevant prey items in terms of prey number (*N*). The order of the items in the table is according to prey number (*N*).

Country	Year	Habitat cover	Relevant prey items (*N*)	Reference
Colombia	2012	Pasture lands	Isoptera, Formicidae, Acari	González-Duran *et al.* 2012
Colombia	2013	Pasture lands	*Digitonthophagus gazella*	Blanco-Torres *et al.* 2013
Venezuela	2019	No data	Isoptera, Formicidae, Lepidoptera, Araneae	Cañizales 2019
Colombia	2020	Pasture lands	Isoptera, Acari, Formicidae	Atencia *et al.* 2020
Venezuela	2020	Agricultural and pasture lands	Isoptera, Acari, Formicidae	Viña-Albornoz *et al.* 2020
Colombia	2021	Agricultural and pasture lands	Isoptera, Formicidae	Blanco-Torres *et al.* 2021a
Colombia	2022	Pasture lands	Acari, Isoptera, Formicidae	This study

pustulosus from the Middle Magdalena River valley and evaluated the relationship between anuran morphometric measurements and prey size and volume. We found 37 individuals with prey items and 21 individuals with empty stomachs. This result could be due to the beginning of the breeding season (Hirai and Matsui 2000), during which males spend more time calling and searching for females and consequently less time foraging for food. In this context, *Engystomops* and congeners breed from April to December (Ryan *et al.* 1983), and we captured the males in our study during April.

Our data indicated that *E. pustulosus* consumes arthropods as do most anurans (Parmelee 1999, Narvaez and Ron 2013, Womack and Bell 2020), with the exception of a few species that have been reported to prey on vertebrates such as birds, rodents, and other amphibian species (Santos *et al.* 2004, Caicedo-Martínez *et al.* 2021). This pattern is not surprising because invertebrates are an abundant resource in almost all ecosystems and represent an advantageous food source because of the low energetic costs associated with their capture and consumption (Taigen and Pough 1983, Biavati *et al.* 2004, Vitt and Caldwell 2014, Pacheco *et al.* 2017).

The greater occurrence of Isoptera, Acari, and Formicidae found in the studied population of *E. pustulosus* was similar to the diet of the species throughout its range (Gonzalez-Duran *et al.* 2012, Blanco-Torres *et al.* 2021a, b). This species is terrestrial and can be found in open habitats including pastures (Ospina-L and Bedoya-Cañón 2018), and termites, ants, and mites typically occur in large numbers in these habitats. In this sense, *Engystomops* and the closely related genus *Physalaemus* (Leptodactylidae; Lourenço *et al*. 2015) can be classified as specialists of small prey such as termites or ants (Duellman 1978, Vitt and Caldwell 1994, Parmelee 1999, Narvaez and Ron 2013, Almeida *et al.* 2019). The lack of correlation between morphometric measurements and prey number or prey volume found in this study may be explained by the higher proportion of termites, ants, and mites even though morphologically they could consume larger prey (Guzman and Salazar 2012).

Table 3. Data (%N) on prey types and total prey consumed by *Engystomops pustulosus* obtained from the published literature and the present work. Sources: (1) González-Duran *et al.* 2012; (2) Cañizales 2019; (3a) Atencia *et al.* 2020; locality: Santa Inés; (3b) Atencia *et al.* 2020; locality: Coloso; (3c) Atencia *et al.* 2020; locality: El Roble; (4) Viña-Albornoz *et al.* 2020; (5) Blanco-Torres *et al.* 2021a; (6) this study. Undetermined prey items (und.) are noted when higher taxonomic resolution was not available. "X" represents the presence of prey in the stomach contents.

Prey taxa	Sources of data on prey categories							
	1	2	3a	3b	3c	4	5	6
ARTHROPODA								
Arachnida								
Acari und.	9.6					0.51	9.68	
Ixodida								
Argasidae						0.11		
Trombidiformes und.			10.67	23.29	5.16	29.48		
Trombidiidae						0.15		
Oribatida								
Ceratozetidae								0.5
Trhypochthoniidae								48.25
Araneae und.		X					0.65	0.25
Theridiidae						0.04		
Pseudoscorpiones und.						0.07	0.08	
Chilopoda	0.4							
Diplopoda und.	0.1					0.15		
Polydesmida								
Fuhrmanodesmidae								0.25
Crustacea								
Isopoda						0.84	0.98	
Insecta								
Collembola und							0.08	
Dycirtomidae	1.5							
Isotomidae						0.7		
Sminthuridae						0.92		
Blattodea								
Ectobiidae						0.04		
Coleoptera und.							0.9	
Anobiidae						0.04		
Carabidae						0.04		
Chrysomelidae	0.1							0.25
Coccinellidae						0.04		
Curculionidae			0.56			0.04		
Dytiscidae			0.56	0.24				
Elateridae						0.26		
Lampyridae						0.07		
Mycetophagydae	0.2							
Nitidulidae	0.1							

Table 3. *Continued.*

Prey taxa	Sources of data on prey categories							
	1	2	3a	3b	3c	4	5	6
Passalidae						0.11		
Scarabaeidae	0.1		0.56					
Silvanidae	0.2							
Staphylinidae	0.5		1.12			0.52		1
Tenebrionidae			1.12	0.24				
Trogossitidae	0.1							
Diptera und.							0.16	
Ceratopogonidae						0.47		
Chironomidae	0.1							
Dolichopodidae						0.04		
Drosophilidae	0.6							
Ephydridae						0.08		
Micropezidae	0.4							
Phoridae						0.04		
Psychodidae	1							
Sphaeroceridae	6					0.07		
Stratiomydae						0.04		
Tephritidae						0.07		
Hemiptera und.							0.24	
Cicadellidae	0.1							
Fulgoridae	0.2							
Miridae						0.07		
Tingidae						0.07		
Hymenoptera und.						0.04	16.48	
Diapriidae	0.1							
Figitidae	0.1							0.25
Formicidae	18.8	X	39.89	0.71	1.07	9.94		8
Isoptera und.		X					70.3	
Kalotermitidae								17.75
Termitidae	59.4		43.82	75.06	94.72	54.09		23.25
Lepidoptera		X				0.08		
Orthoptera und.							0.16	
Psocoptera								
Psocidae			0.56			0.04		
Thysanoptera								
Thripidae	0.1							
MOLLUSCA und.	0.1					0.51	0.08	
Pulmonata								0.25
Physidae			0.56	0.24				
Total prey items in each study	**1061**		**178**	**426**	**833**	**2727**	**1219**	**400**

Despite the dominance of termites, ants, and mites in the stomach contents across geographic localities, we found a shift in the taxonomic identity of other prey items. We found that 66 prey items were consumed among different studies of the diet of *E. pustulosus*. Unique prey items were found in specific localities (Atencia *et al.* 2020, Viña-Albornoz *et al.* 2020). Changes in consumption of prey items showed that the diet of *E. pustulosus* can have plasticity across different localities (Atencia *et al.* 2020), possibly due to differences in spatial and temporal variables in prey availability (Agudelo-Cantero *et al.* 2015). For example, rainy seasons could affect the humidity of topsoil layers, a determining factor for the abundance and presence of mites. Rainy periods may also affect the production of vegetation and foliage consumed by many species of termites and ants. This study included different years and seasons (i.e., rainy or dry seasons), and geographical localities with changes in habitat covers (*e.g*., more or less disturbance in cattle pastures or agricultural development). These parameters clearly affect the presence of different prey items. To our knowledge, no information about prey availability is available to corroborate this assumption.

We encourage further assessment of major geographic localities to better understand the composition of prey consumed by this anuran species. It is also key to study prey availability (*e.g*., del Rio-García *et al.* 2014) and dietary variation in response to spatial and temporal changes (*e.g*., Blanco-Torres *et al.* 2021a, López-Bedoya *et al.* 2022b). The distribution and composition of invertebrate communities differ between natural and anthropic ecosystems, and between rainy and dry periods (*e.g*., Ospina-Bautista *et al.* 2022). Given the importance of predator-prey interactions for stability and energy flow in different natural and anthropogenic ecosystems, further insight on broader knowledge gaps (*e.g*., land-use change and prey availability) may aid understanding predator-prey interactions in anthropogenic environments (*i.e*., plantations, pastures; Konopik *et al.* 2014, Moskowitz *et al.* 2020).

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References

Adis, J. (ed.) 2002. *Amazonian Arachnida and Myriapoda: Identification Keys to all Classes, Orders, Families, Some Genera, and Lists of Known Terrestrial Species*. Bulgaria. Pensoft Publishers. 588 pp.

Agudelo-Cantero, G. A., R. S. Castaño-Valencia, F. Castro-Herrera, L. Fierro-Pérez, and H. Asencio-Santofimio. 2015. Diet of the blue-bellied poison frog *Andinobates minutus* (Anura: Dendrobatidae) in two populations from the Colombian Pacific. *Journal of Herpetology 49:* 452–461.

Almeida, B. C., R. S. Santos, T. F. Santos, M. B. Souza, and M. Menin. 2019. Diet of five anuran species in a forest remnant in eastern Acre state, Brazilian Amazonia. *Herpetology Notes 12:* 945–952.

Arnett, R. H. and M. C. Thomas (eds.). 2000. *American Beetles, Volume I: Archostemata, Myxophaga, Adephaga, Polyphaga: Staphyliniformia*. Boca Raton. CRC Press. 464 pp.

Atencia, P., L. Solano, and J. Liria. 2020. Morphometric differentiation and diet of *Engystomops pustulosus* (Amphibia: Leptodactylidae) in three populations from Colombia. *Russian Journal of Herpetology 27:* 156–164.

Badejo, M. A., S. Woas, and L. Beck. 2002. Redescription of *Archegozetes magnus* (Sellinick, 1925) (Trhypochthonioidea) from Brazil and description of two new species of nanhermanniid mites: *Bicyrthermannia nigeriana* and *Masthermannia seropedica* (Nanhermannioidea) (Acari: Oribatida). *Genus 14:* 125–149.

Balogh, J. and P. Balogh. 1988. *Oribatid Mites of the Neotropical Region I*. Budapest. Akadémiai Kiadó. 335 pp.

Balogh, J. and P. Balogh. 1990. *Oribatid Mites of the Neotropical Region II*. Budapest. Akademiai Kiadó. 333 pp.

Barrio-Amorós, C. L., F. J. M. Rojas-Runjaic, and J. C. Señaris. 2019. Catalogue of the amphibians of Venezuela: illustrated and annotated species list, distribution, and conservation. *Amphibian and Reptile Conservation 13:* 1–198 (e180).

Biavati, G. M., H. C. Wiederhecker, and G. R. Colli. 2004. Diet of *Epipedobates flavopictus* (Anura: Dendrobatidae) in a Neotropical savanna. *Journal of Herpetology 38:* 510–518.

Blanco-Torres, A., M. Duré, and M. A. Bonilla-Gómez. 2021a. Trophic relationships among five species of Anura in the Colombian Caribbean tropical dry forest: a spatial and temporal approach. *South American Journal of Herpetology 19:* 22–31.

Blanco-Torres, A., M. Duré, and M. A. Bonilla. 2021b. Anurans trophic dynamic and guild structure in tropical dry forests of the Caribbean region of Colombia. *Anais da Academia Brasileira de Ciências 93:* e20201022.

Blanco-Torres, A., M. I. Duré, M. A. Bonilla, and L. Cagnolo. 2020. Predator-prey interactions in anurans of the tropical dry forests of the Colombian Caribbean: A functional approach. *Biotropica 52:* 730–737.

Blanco-Torres, A., K. Navarro, C. Solís, L. C. Gutiérrez, and M. A. Bonilla. 2013. Anuros del bosque seco tropical (Caribe Colombiano) ingieren al escarabajo exótico *Digitonthophagus gazella* (Scarabaeinae: Onthophagini). *Entomotropica 28:* 227–232.

Caicedo-Martínez, L. S., S. Escobar-Lasso, J. C. Zuluaga-Isaza, C. Londoño-Quiceno, J. G. Orrego-Meza, and J. M. Rivera-Pérez. 2021. Review of post-metamorphic frog-eat-frog predation, with a description of a new cases of anurophagy. *Food Webs 27:* e00191.

Cañizales, I. 2019. Contenido estomacal en anuros de la Cordillera de la Costa de Venezuela. *Acta Biologica Venezuelica 39:* 125–136.

Cardona, F. A., F. David, and S. E. Hoyos. 2010. *Flora de La Miel, Central Hidroeléctrica Miel I, Oriente de Caldas, Guia ilustrada*. Medellín, Colombia. ISAGEN - Universidad de Antioquia, Herbario Universidad de Antioquia (HUA). 228 pp.

Cloyed, C. S. and P. K. Eason. 2017. Niche partitioning and the role of intraspecific niche variation in structuring a guild of generalist anurans. *Royal Society Open Science 4:* 170060.

Cole, C. J., C. R. Townsend, R. P. Reynolds, R. D. MacCulloch, and A. Lathrop. 2013. Amphibians and reptiles of Guyana, South America: Illustrated keys, annotated species accounts, and a biogeographic synopsis. *Proceedings of the Biological Society of Washington 125:* 317–578.

Colón-Gaud, C., M. R. Whiles, S. S. Kilham, K. R. Lips, C. M. Pringle, S. Connelly, and S. D. Peterson. 2009. Assessing ecological responses to catastrophic amphibian declines: Patterns of macroinvertebrate production and food web structure in upland Panamanian streams. *Limnology and Oceanography 54:* 331–343.

Connelly, S., C. M. Pringle, R. J. Bixby, R. Brenes, M. R. Whiles, K. R. Lips, S. Kilham, and A. D. Huryn. 2008. Changes in stream primary producer communities resulting from large-scale catastrophic amphibian declines: Can small-scale experiments predict effects of tadpole loss? *Ecosystems 11:* 1262–1276.

Del Rio-García, J. S., V. H. Serrano-Cardozo, and M. P. Ramírez-Pinilla. 2014. Diet and microhabitat use of *Bolitoglossa* cf. *pandi* (Caudata: Plethodontidae) from the Cordillera Oriental of Colombia. *South American Journal of Herpetology 9:* 52–61.

Doan, T. M. 2003. Which methods are most effective for surveying rain forest herpetofauna? *Journal of Herpetology 37:* 72–81.

Duellman, W. E. 1978. The biology of an equatorial herpetofauna in Amazonian Ecuador. *The University of Kansas Museum of Natural History, Miscellaneous Publications 65:* 1–352.

Dunham, A. E. 1983. Realized niche overlap, resource abundance, and intensity of interspecific competition. Pp. 261–280 *in* R. B. Pianka and T. Schoener (eds.), *Lizard Ecology: Studies of a Model Organism*. Cambridge. Harvard University Press.

Eisenhauer, N., A. Milcu, E. Allan, N. Nitschke, C. Scherber, V. Temperton, A. Weigelt, W. W. Weisser, and S. Scheu. 2011. Impact of above- and below-ground invertebrates on temporal and spatial stability of grassland of different diversity. *Journal of Ecology 99:* 572–582.

Fernández, F. (ed.). 2003. *Introducción a las Hormigas de la Región Neotropical*. Bogotá. Instituto de Investigación de Recursos Biológicos Alexander Von Humboldt. 398 pp.

Fernández, F., V. Castro-Huertas, and F. Serna. 2015. *Hormigas Cortadoras de Hojas de Colombia: Acromyrmex & Atta (Hymenoptera: Formicidae)*. Fauna de Colombia, Monografía No. 5. Bogotá D.C., Colombia. Instituto de Ciencias Naturales, Universidad Nacional de Colombia. 350 pp.

Fernández, F., R. J. Guerrero, and T. Delsinne (eds.). 2019. *Hormigas de Colombia*. 1st ed. Bogotá. Universidad Nacional de Colombia. 1200 pp.

González-Duran, G., P. D. A. Gutiérrez-Cárdenas, and S. Escobar-Lasso. 2012. *Physalaemus pustulosus* (Tungara frog). Diet. *Herpetological Review 43:* 124–125.

Gutiérrez-Cárdenas, P. D. A., K. Castillo, D. Martínez, C. F. D. Rocha, and M. A. Rojas-Rivera. 2016. Trophic ecology of *Pristimantis labiosus* (Anura: Craugastoridae) from South-Western Colombia. *North-Western Journal of Zoology 12:* 102–109.

Guzmán P. A. and J. C. Salazar. 2012. Una aproximación estadística para explorar la relación entre la morfometría de unas ranas colombianas y sus hábitos alimenticios. *Revista de la Facultad de Ciencias Universidad Nacional de Colombia, Sede Medellín 1:* 23–39.

Hirai, T. and M, Matsui. 2000. Feeding habits of the Japanese tree frog, *Hyla japonica*, in the reproductive season. *Zoological Science 17:* 977–982.

Ings, T. C., J. M. Montoya, J. Bascompte, N. Blüthgen, L. Brown, C. F. Dormann, F. Edwards, D. Figueroa, U. Jacob, J. I. Jones, R B. Lauridsen, M E. Ledger, H. M. Lewis, J. M. Olesen, F. J. F. van Veen, P. H. Warren, and G. Woodward. 2009. Ecological networks - beyond food webs. *Journal of Animal Ecology 78:* 253–269.

Ješovnik, A. and T. R. Schultz. 2017. Revision of the fungus-farming ant genus *Sericomyrmex* Mayr (Hymenoptera, Formicidae, Myrmicinae). *ZooKeys 670:* 1–109.

Köhler, G. 2011. *Amphibians of Central America*. Offenbach. Herpeton, Verlag. 379 pp.

Konopik, O., C. L. Gray, T. U. Grafe, I. Steffan-Dewenter, and T. M. Fayle. 2014. From rainforest to oil palm plantations: Shifts in predator population and prey communities, but resistant interactions. *Global Ecology and Conservation 2:* 385–394.

Laigle, I., I. Aubin, C. Digel, U. Brose, I. Boulangeat, and D. Gravel. 2018. Species traits as drivers of food web structure. *Oikos 127:* 316–326.

López-Bedoya, P. A., M. Bohada-Murillo, M. C. Angel-Vallejo, L. D. Audino, A. L. V. Davis, G. Gurr, and J. A. Noriega. 2022a. Primary forest loss and degradation reduces biodiversity and ecosystem functioning: A global meta-analysis using dung beetles as an indicator taxon. *Journal of Applied Ecology 59:* 1572–1585.

López-Bedoya, P. A., E. A. Cardona-Galvis, J. N. Urbina-Cardona, F. A. Edwards, and D. P. Edwards. 2022b. Impacts of pastures and forestry plantations on herpetofauna: A global meta-analysis. *Journal of Applied Ecology 59:* 3038–3048.

López-Bedoya, P. A., T. Magura, F. A. Edwards, D. P. Edwards, J. M. Rey-Benayas, G. L. Lövei, and J. A. Noriega. 2021. What level of native beetle diversity can be supported by forestry plantations? A global synthesis. *Insect Conservation and Diversity 14:* 736–747.

Lourenço, L. B., C. P. Targueta, D. Baldo, J. Nascimento, P. C. A. Garcia, G. V. Andrade, C. F. B. Haddad, and S. M. Recco-Pimentel. 2015. Phylogeny of frogs from the genus *Physalaemus* (Anura, Leptodactylidae) inferred from mitochondrial and nuclear gene sequences. *Molecular Phylogenetics and Evolution 92:* 204–216.

Maneyro, R. and I. da Rosa. 2004. Temporal and spatial changes in the diet of *Hyla pulchella* (Anura, Hylidae) in southern Uruguay. *Phyllomedusa 3:* 101–103.

Manicom, C. and L. Schwarzkopf. 2011. Diet and prey selection of sympatric tropical skinks. *Austral Ecology 36:* 485–496.

Miranda, T., M. Ebner, M. Solé, and A. Kwet. 2006. Spatial, seasonal and intrapopulational variation in the diet of *Pseudis cardosoi* (Anura: Hylidae) from the Araucaria Plateau of Rio Grande do Sul, Brazil. *South American Journal of Herpetology 1:* 121–130.

Morales-Castilla, I., M. G. Matias, D. Gravel, and M. B. Araújo. 2015. Inferring biotic interactions from proxies. *Trends in Ecology & Evolution 30:* 347–356.

Moroti, M. T., P. T. Soares, M. Pedrozo, D. B. Provete, and D. J. Santana. 2021. The effects of morphology, phylogeny and prey availability on trophic resource partitioning in an anuran community. *Basic and Applied Ecology 50:* 181–191.

Moskowitz, N. A., B. Dorritie, T. Fay, O. C. Nieves, C. Vidoudez, Cambridge Rindge Latin 2017 Biology Class, Masconomet 2017 Biotechnology Class, E. K. Fischer, S. A. Trauger, L. A. Coloma, D. A. Donoso, and L. A. O'Connell. 2020. Land use impacts poison frog chemical defenses through changes in leaf litter ant communities. *Neotropical Biodiversity 6:* 75–87.

Narvaez, A. E. and S. R. Ron. 2013. Feeding habits of *Engystomops pustulatus* (Anura: Leptodactylidae) in Western Ecuador. *South American Journal of Herpetology 8:* 161–167.

Ospina-L, A. M. and M. A. Bedoya-Cañón. 2018. *Engystomops pustulosus* (Cope, 1864). Rana túngara. *Catálogo de Anfibios y Reptiles de Colombia 4:* 7–15.

Ospina-Bautista, F., P. A. López-Bedoya, J. V. Estévez, D. Martínez-Torres, and S. G. Jiménez. 2022. Restoration strategy drives the leaf litter myriapod richness (Arthropoda: Myriapoda) on a protected area. *Boletín Científico, Museo de Historia Natural, Universidad de Caldas 26:* 13–23.

Pacheco, E. O., V. G. Ferreira, R. M. H. Carvalho. 2017. Diet of *Boana albopunctata* (Anura: Hylidae) in an Atlantic

Forest fragment of southeastern Brazil. *Phyllomedusa 16:* 57–62.

Parmelee, J. R. 1999. Trophic ecology of a tropical anuran assemblage. *Scientific Papers, Natural History Museum, The University of Kansas 11:* 1–59.

Perez-Pedraza, L. F. and F. Fernández. 2019. Género *Strumigenys*. Pp. 1069–1088 *in* F. Fernández, R. J. Guerrero, and T. Delsinne (eds.), *Hormigas de Colombia*. Bogotá, Universidad Nacional de Colombia.

Pinkas, L., M. S. Oliphant, and I. L. K. Iverson. 1971. Food habitat of albacore, bluefin tuna, and bonito in California waters. *Fish Bulletin 152:* 1–105.

R Core Team. 2022. R: A language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. URL: http://www.Rproject.org/

Ryan, M. J., G. A. Bartholomew, and A. S. Rand. 1983. Energetics of reproduction in a neotropical frog, *Physalaemus pustulosus*. *Ecology 64:* 1456–1462.

Ryser, R., M. Hirt, J. Häussler, D. Gravel, and U. Brose. 2021. Landscape heterogeneity buffers biodiversity of simulated meta-food-webs under global change through rescue and drainage effects. *Nature Communications 12:* 4716.

Santos, E. M., A. V. Almeida, and S. D. Vasconcelos. 2004. Feeding habits of six anuran (Amphibia: Anura) species in a rainforest fragment in Northeastern Brazil. *Iheringia, Série Zoologia 94:* 433–438.

Solé, M. and D. Rödder. 2010. Dietary assessments of adult amphibians. Pp 167–184 *in* C. K. Dodd Jr. (ed.), *Amphibian Ecology and Conservation*: *A Handbook of Techniques*. Oxford. Oxford University Press.

Taigen, T. L. and F. H. Pough. 1983. Prey preference, foraging behavior, and metabolic characteristics of frogs. *American Naturalist 122:* 509–520.

Triplehorn, C. A. and N. F. Johnson. 2005. *Borror and DeLong's Introduction to the Study of Insects*. 7th ed. Belmont, USA. Thomson/Brooks Cole. 864 pp.

Urbina-Cardona, N., L. Saboyá-Acosta, C. P. Camacho-Rozo, A. R. Acosta-Peña, A. Arenas-Rodríguez, J. F. Albarracín-Caro, A. M. Moreno-Cabal, N. M. Novoa-Salamanca, M. J. Camacho-Durán, N. Giraldo-Echeverry, M. J. Hernández-Gallego, L. Pirateque-López, V. Aldana-Varón, D. Echeverry-Pareja, and F. A. Zabala-Forero. 2023. Producción científica sobre la herpetología en Colombia: perspectivas desde los temas de investigación hacia la conservación biológica. *Caldasia 45:* 1–20.

Viña-Albornoz, J. L., C. Molina, and Z. Tarano. 2020. Prey consumption of the neotropical frog *Engystomops pustulosus* (Anura: Leptodactylidae) in northwestern Venezuela. *Herpetological Conservation and Biology 15:* 272–283.

Vitt, L. J. and J. P. Caldwell. 1994. Resource utilization and guild structure of small vertebrates in the Amazon Forest leaf litter. *Journal of Zoology 234:* 463–476.

Vitt, L. J. and J. P. Caldwell. 2014. *Herpetology: An Introductory Biology of Amphibians and Reptiles*. 4th ed. London. Elsevier. 757 pp.

Whiles, M. R., R. O. Hall, W. K. Dodds, P. Verburg, A. D. Huryn, C. M. Pringle, K. R. Lips, S. S. Kilham, C. Colón-Gaud, A. T. Rugenski, S. Peterson, and S. Connelly. 2013. Disease-driven amphibian declines alter ecosystem processes in a tropical stream. *Ecosystems 16:* 146–157.

Womack, M. C. and R. C. Bell. 2020. Two-hundred million years of anuran body-size evolution in relation to geography, ecology and life history. *Journal of Evolutionary Biology 33:* 1417–1432.

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