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ORIGINAL ARTICLE

What size of Neotropical frogs do spiders prey on?

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Abstract

Interactions between vertebrates and invertebrates at similar trophic levels can shape community diversity and interactions, being frogs acting as prey and predators. Although spiders are a common dietary item for anurans, reports of frog predation by spiders are increasingly common in the literature. Anurans are preyed by several arthropod taxa, and spiders are, by far, the most important invertebrate predator for the group. Herein we report six new predation events by spiders on frogs and, based on a literature review, we analyzed the relationship between frog and spider sizes, and on prey niche overlap between frog and spider families for the Neotropics. Records of predation increased substantially in the last decades, especially after 2005. We recovered a relationship between frog and spider sizes, with the spider predator similar-sized or smaller than frogs. Most anuran prey ranged from 15 to 25 mm in body size, while most spiders were about 53% smaller than the frogs. Spiders were not specialized in any anuran family. Large cursorial spiders were involved in most of the reports, especially Ctenidae spiders, and Hylidae was the most frequently predated frog family. Since this prey-predator relationship is often determined by size, spiders may avoid larger frogs, explaining the pattern of our recovered reports of predation on smaller frogs. Although common, we suggest that future reports on spider-frog predation events should include more information, such as prey/predator sizes and identification, anti-predator strategies, time for capture and ingestion, anuran stage, and habitat characteristics.

Keywords Kernel density · Predation events · Predation probability · Size-constrained predation

Introduction

Interactions among predators and prey are a key ecological factor in nature, shaping community structure and regulating competitive interactions within populations and between species (Morin 1986; Temple 1987; Duellman and Pianka 1990; Bohannan and Lenski 2000; Roslin et al. 2017). Amphibians, like many other animals, have dual roles in food webs, having diets largely composed of invertebrates (Duellman and Trueb 1994; Verburg et al. 2007), and being preyed upon by several vertebrates, such as snakes, mammals, other amphibians, and birds (Duellman and Trueb 1994). Anurans occupy an important position in food webs as a link between invertebrates and vertebrates because many predators of amphibians rarely prey on invertebrates (Toledo et al. 2007). Thus, anurans promote the energy flow from low-level invertebrates to higher-level vertebrates (Verburg et al. 2007).

The relevance of the position in food webs is markedly dominant in Neotropical ecosystems, where anurans are diverse and abundant, and an important food source for generalist predatory invertebrates, such as spiders (Menin et al. 2005; Toledo 2005; Von May et al. 2019; Nyffeler and Altig 2020; Valdez 2020). Reports of anuran predation by spiders are common (Menin et al. 2005; Folt and Lapinski 2017; Costa-Campos et al. 2018; Von May et al. 2019; Lira et al. 2020; Nyffeler and Altig 2020; Valdez 2020), suggesting that this relationship may be relevant in Neotropical ecosystems, regulating community structure. Predation events between frogs and spiders usually involve a typical sit-and-

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wait predator (Uetz 1992) accessing valuable prey, such as amphibians, reptiles, and mammals (McCormick and Polis 1982; Valdez 2020). Although spiders are commonly eaten by Neotropical frogs (Toft 1980; Lima and Magnusson 1998; Parmelee 1999; Biavati et al. 2004; Garda et al. 2007; Magalhães et al. 2016; Ceron et al. 2018; Marques-Pinto et al. 2019), they can also be one of the most important invertebrate predators of vertebrates (McCormick and Polis 1982; Valdez 2020), suggesting a complex system mediated by predatory relationships at a similar trophic level (e.g. Brodie III and Brodie 1999). Individual prey or predator body size can affect the outcome of predatory interactions (Polis et al. 1989; Polis and Holt 1992; Brodie III and Brodie 1999), where the size of either individual can change the predator/prey status of individuals and lead to the reversal of outcomes during interactions (Lima et al. 2006). Therefore, studies focusing on the effects of predator and prey body sizes in predatory interactions are useful for understanding the dynamics of predatory interactions.

Here, we provide a literature review and new analyzes on the prey-predator relationship between frogs and spiders in the Neotropical region. We (1) provide six new observations of spiders preying upon frogs in the Neotropical region; (2) tested the relationship in sizes of spiders and frogs, to see if there is a relationship between prey and predator sizes; (3) evaluated the reported frequency in sizes of spiders and frogs, based on previously reported events, to observe which sizes of anurans are the most preyed-upon, and which size of predatory spiders are the most involved in those events; and (4) tested taxonomic patterns in predator-prey relationships between frogs and spiders, considering the circumstantial importance of frogs as prey for several spider families. We tested for a relationship between spider and frog sizes, and also if different prey capture strategies observed within different spider families (Uetz 1992; Nyffeler 1999) are more efficient toward different frog families.

Materials and methods

Field observations and new predation records

We made novel observations of spider-frog interactions in several fieldworks conducted in the years 2004, 2008, 2009, 2014, 2016, and 2018, in the states of Acre, Distrito Federal, Goiás, Minas Gerais, Rondônia, and São Paulo, which during the search for reptiles and amphibians, the predation events were opportunistically registered. The specimens were identified based on guides and specialized literature (Lutz 1973; Caramaschi and Pombal 2001; Brescovit et al. 2011; Bernarde et al. 2013; Brusquetti et al. 2013; Motta 2014; Fukushima and Bertani 2017). None of the individuals were collected.

Bibliographic review

To review published papers describing predatory events of spiders on frogs, we searched for published papers on Google Scholar and the Scientific Electronic Library Online (Scielo) using the following terms and combinations of them: "Spider, Araneae, Frog, Anura, predation attempt, prey, Neotropical, Brazil, Cerrado, Atlantic Forest, Amazonia, Neotropics, New-World". We also searched for papers in archives of four journals that publish natural history notes: Herpetological Bulletin, Herpetology Notes, Herpetological Review, and Mesoamerican Herpetology.

Data analysis

To understand the effect of the size of predators and preys in frog-spider interactions, we used a non-parametric Kernel density approach (Rosenblatt 1956; Parzen 1962) to describe a probability density function. We plotted the values and calculated the probability density with paired data (spider and predated anuran size) of each literature record using the wesanderson package (version 0.3.6, 2018, Ram and Wickham 2018) in the R environment, version 3.5.1 (R Core Team 2019). For this analysis, we used only data gathered from peer-reviewed journals providing both anuran and spider sizes. We used cephalothorax + abdomen length for spider size and snout-vent length (SVL) for frog size.

For the calculation of the Kernel probability density, we assume that X_1, X_2, … X_i is a sequence of independent random variables selected from a distribution with bounded density $\widehat{f}$, a kernel estimator for $\widehat{f}(x)$ is provided by:

$$\widehat{f}(x) = \frac{1}{nh} \sum_{i=1}^{n} K(x - x_i)$$

Where K is Kernel (a non-negative function, h is the bandwidth of the function and n is the total number of observations.

We also evaluated prey niche overlap between spider families on frog families to test if there is a specialization on certain anuran families or if spiders are generalist anuran predators because frog size can vary greatly by taxonomic family. We made this analysis using the Pianka index:

$$\alpha = {}^{\Sigma U1j * U2j} / {}_{\Sigma (U1j) * (U2j) * \alpha^{2\cdot}}$$

Where $U1j$ is the proportion of resource j use by species 1 and $U2j$ refers to the proportion of resource j use by species 2 (Pianka 1973). We evaluated if observed niche overlap was smaller than expected by chance using the module Niche Overlap in the package 'ECOSIM R' in software R, with 1000 randomizations. We used the algorithm RA2, which is used when, even in the absence of species interactions, some resources are not available to some species (Gotelli and Entsminger 2003). If the spiders are partitioning dietary resources (anuran families), the variance on the observed niche overlap should be smaller than the observed overlap simulated by chance.

Results

Field observations and new predation records

We report six new records, involving four frog families (Brachycephalidae, Craugastoridae, Hylidae, and Leptodactylidae) and three spider families (Ctenidae, Lycosidae, and Theraphosidae). On 16 September 2004, we observed a *Barycholos ternetzi* (Miranda-Ribeiro, 1937) being preyed upon by a *Ctenus* sp., on the margin of a stream inside a mesophytic semi-deciduous forest remnant located in the municipality of Campos Belos, Goiás state, Brazil (13°02' S, 46°46' W, 643 m a.s.l). The predation was first observed at 13:00 h, and the spider was using its chelicerae to hold the frog by its left flank (Fig. 1a). After about 10 min of struggling, the frog died.

On 16 December 2008, we observed a *Pristimantis* sp. being preyed on by an *Ancylometes* sp., on the leaf litter in a forest remnant in the municipality of Porto Velho, Rondônia state, Brazil (08°45' S, 63°54' W, 85 m a.s.l). The predation was first noticed at 19:27 h, and the spider was dragging the dead frog, holding it by its neck with its chelicerae (Fig. 1b).

On 22 May 2009, we recorded a *Boana raniceps* (Cope, 1862) being preyed on by an *Avicularia* sp., on a light pole in a periurban area of the municipality of Cruzeiro do Sul, Acre state, Brazil (07°37' S, 72°40' W, 182 m a.s.l.). The predation was first noticed at 20:30 h, and the spider was holding the frog by the dorsal part of its neck, using its chelicerae, while hanging in the post (Fig. 1c). After some struggling, the frog died.

On 21 December 2014, we recorded a *Physalaemus* sp. being preyed on by *Ancylometes* sp., on the ground in a forest remnant in the municipality of Cruzília, Minas Gerais state, Brazil (21°50' S, 44°48' W, 1010 m a.s.l). The predation was first noticed at 20:41 h, and the frog was struggling, trying to release itself, while the spider held it by the left leg with its chelicerae (Fig. 1d). After some struggling, the frog died.

On 16 September 2016, we recorded an *Ischnocnema parva* (Girard, 1853) being preyed on by a *Ctenus* cf. *ornatus* (Keyserling, 1877), on the leaf litter in a forest remnant at Serra da Cantareira, municipality of São Paulo, São Paulo state, Brazil (23°24' S, 46°35' W, 1181 m a.s.l). The predation was first noticed at 18:52 h, and the frog was trying to release himself, while the spider held it by the neck, using its chelicerae (Fig. 1e). After a while, the frog died.

On 10 October 2018, we recorded a froglet of *Boana albopunctata* (Spix, 1824) being preyed on by an adult lycosid spider *Aglaoctenus lagotis* (Holmberg, 1876) on the outer margin of its web, in an open field at Fazenda Água Limpa, Distrito Federal, Brazil (15°58' S, 47°55' W, 1178 m a.s.l.). The spider's web was 120 cm above the ground, attached to some branches in a groove close to a permanent pond. We first notice the predation event at 19:40 h, and the froglet was still alive and struggling, trying to release itself, while the spider was holding it by the neck using its chelicerae (Fig. 1f). After four minutes, the spider dragged the frog to the interior part of the funnel-web.

Bibliographic review

We found 93 papers describing predation of anurans by spiders, representing 36 genera of anurans from 14 families, and 27 genera of spiders, from 11 families, describing 134 predatory events, being the first report published in 1978 and the more recent ones in 2020 (Table 1). The number of reports of predation on frogs by spiders are increasing fast, especially after 2005 (Fig. 2). Most observations (80%) described predation on adult anurans, while 25 events were on tadpoles or juveniles (18%). The other events did not address the anuran developmental stage. In 16 predation events, the spider species and genus was not identified, and in three events the anuran species and genus were not identified (Table 1). Regarding anurans, the most preyed upon families were Hylidae (65 records, 48%) and Leptodactylidae (20 records, 14%). Among anuran genera, the higher number of predation events was reported for *Dendropsophus*, corresponding to 28 records (21%) for 16 different species. The species most frequently recorded to be predated by spiders was *Dendropsophus minutus* (Peters, 1872) (nine reported cases, 7%). Among spiders, the family Ctenidae accounted for more than half of the events (71 records, 53%), followed by Pisauridae with 15 records (11%) (Table 1). The genus *Ancylometes* (Ctenidae) accounted for 35 predation events (26%) and was the most frequent frog-eating spider genus. The biggest frog killed was a *Rhinella marina* (Linnaeus, 1758) (Bufonidae; 90.5 mm SVL) by a *Theraphosa blondi* (Latreile, 1804) (Theraphosidae; 84.1 mm), followed by *Leptodactylus knudseni* Heyer, 1972 (Leptodactylidae, 90 mm SVL), and preyed upon by the same spider species. The smallest frog predated was a 6 mm *Dendrobates auratus* (Girard, 1855) (Dendrobatidae) by a *Sericopelma rubronitens* Ausserer, 1875 (Theraphosidae; average size = 45 mm).

The size range of spiders varied more than frogs during the predator-prey interactions. During the review of predation events, frogs were often larger than spiders. Although we found 134 observations of frog predation by spiders on

Fig. 1 **a** *Barycholos ternetzi* being preyed upon by *Ctenus* sp. **b** *Pristimantis* sp. being preyed upon by *Ancylometes* sp. **c** *Boana raniceps* being preyed upon by *Avicularia* sp. **d** *Physalaemus* sp. being preyed upon by *Ancylometes* sp. **e** *Ischnocnema parva* being preyed upon by *Ctenus* cf. *ornatus*. **f** Froglet of *Boana albopunctata* being preyed upon by *Aglaoctenus lagotis*. Photographed by: a Sérgio Brant, b and f by Saymon de Albuquerque, d by Henrique Nogueira, e by Victor Fávaro Augusto and f by Afonso S. O. Meneses

Neotropics, only 51 reports (ca. 38%) presented prey and predator sizes. We performed a linear model aiming to evaluate predator and prey size relationships. There is a positive relationship between spider and frog size ($y = 0.7x + 9.34$; $r^2 = 0.348$; $p = 0.0007$), showing that bigger spiders can capture larger frogs (Fig. 3). Most recorded events ranged from 15 mm to 25 mm in body size in anurans (Figs. 4 and 5), however, spider predators were smaller than preyed frogs, being frogs 53% larger than spiders on average (Fig. 5).

Relationship between spider and frog families

The diet overlap between spider families was larger than that expected by chance (mean of simulated index = 0.176; observed index = 0.276; $p < 0.217$).

Discussion

The lycosid *Aglaoctenus lagotis* is a medium-sized spider (1 to 2.3 cm), common in the Cerrado biome (Stefani et al. 2011). The species present a characteristic funnel web, representing an unusual foraging strategy within the Lycosid family (González et al. 2013; Motta 2014). This is not the first record of amphibian predation by *Aglaoctenus* spiders (see Abegg et al. 2014), but we are unaware of previous reports of predation by *A. lagotis* on vertebrates. This observation can be related to the opportunistic foraging of the spider *A. lagotis* (Motta 2014), that can prey only on small-sized frogs, as *Boana albopunctata* froglets, due to the large size of the species' adults (Araújo et al. 2007). The genus *Avicularia* Lamarck, 1818 is composed of arboreal species of

Table 1 Neotropical anurans species preyed by spiders gathered from the literature

Anuran species	SVL (mm)	Spiders	Size (mm)	Reference source
Aromobatidae				
Allobates bruneus (Cope, 1887)	NA	Ctenidae (Unidentified species)	NA	Carvalho et al. (2013)
Anomaloglossus stepheni (Martins, 1989)	18.40	*Ctenus amphora* Mello-Leitão, 1930 (Ctenidae)	16.40	Menin et al. (2005)
Bufonidae				
Amazophrynella minuta (Melin, 1941)	22.00	*Ancylometes rufus* (Walckenaer, 1837) (Ctenidae)	30.00	Menin et al. (2005)
Amazophrynella minuta	15.80	*Ancylometes rufus* (Ctenidae)	9.00	Pazin (2006)
Rhinella granulosa (Spix, 1824)	70.00*	*Phoneutria* sp. (Ctenidae)	NA	Silva-Silva et al. (2013)
Rhinella beebei (Gallardo, 1965)	61.00*	*Ancylometes bogotensis* (Keyserling, 1877) (Ctenidae)	NA	White (2015)
Rhinella marina (Linnaeus, 1758)	90.52	*Theraphosa blondi* (Theraphosidae)	84.12	Menin et al. (2005)
Rhinella ornata (Spix, 1824)	15.00	*Lycosa erythrognata* Lucas, 1836 (Lycosidae)	31.00	Almeida et al. (2010)
Brachycephalidae				
Ischnocnema parva (Girard, 1853)	23.00*	*Ctenus* cf. *ornatus* (Ctenidae)	NA	Present study
Ischnocnema cf. *parva*	15.40	*Oligoctenus medius* (Keyserling, 1891) (Ctenidae)	31.00	Pontes et al. (2009)
Craugastoridae				
Barycholos ternetzi (Miranda-Ribeiro, 1937)	25.61*	*Ctenus* sp. (Ctenidae)	NA	Present study
Barycholos ternetzi	25.61*	*Phoneutria nigriventer* (Keyserling, 1891) (Ctenidae)	NA	Costa et al. (2006)
Craugastor ranoides (Cope, 1886)	NA	*Ancylometes bogotensis* (Ctenidae)	NA	Zumbado-Ulate et al. (2009)
Craugastor stejnegerianus (Cope, 1893)	15.00*	*Cupiennius coccineus* Pickard-Cambridge, 1901(Trechaleidae)	8.00	Ervin et al. (2007)
Craugastor stejnegerianus	15.00*	*Cupiennius coccineus* (Trechaleidae)	8.00	Ervin et al. (2007)
Pristimantis cerasinus (Cope, 1875)	NA	*Trichonephila clavipes* (Linnaeus, 1767) (Araneidae)	NA	Ganong and Folt (2015)
Pristimantis ramagii (Boulenger, 1888)	21.10	*Ancylometes rufus* (Ctenidae)	20.10	De-Carvalho et al. (2010)
Pristimantis ridens (Cope, 1866)	30.00	Ctenidae (Unidentified species)	NA	Jablonski (2015)
Pristimantis ridens	23.00	*Cupiennius coccineus* (Trechaleidae)	NA	Folt and Lapinski (2017)
Pristimantis ridens	20.00*	*Cupinennius* sp. (Trechaleidae)	13.00	Folt and Lapinski (2017)
Pristimantis sp.	NA	*Ancylometes* sp. (Ctenidae)	NA	Present study
Centrolenidae				
Espadarana prosoblepon (Boettger, 1892)	25.00*	*Cupiennius* sp. (Trechaleidae)	33.00*	Hayes (1983)
Hyalinobatrachium colymbiphyllum (Taylor, 1949)	Na	Anyphaenidae (Unidentified species)	Na	Delia et al. (2019)
Teratohyla spinosa (Taylor, 1949)	20.00*	*Eriophora* sp. (Araneidae)	NA	Folt and Lapinski (2017)
Teratohyla spinosa	20.00	*Ancylometes bogotensis* (Ctenidae)	NA	Folt and Lapinski (2017)
Teratohyla spinosa	20.00*	Anyphaenidae (Unidentified species)	NA	Delia et al. (2019)
Cycloramphidae				
Cycloramphus baraceiensis Heyer, 1983	20.00	*Trechaleoides biocellata* (Mello-Leitão, 1926) (Trechaleidae)	50.00	Gaiarsa et al. (2012)
Thoropa miliaris (Spix, 1824)	NA	*Cteniza* sp. (Ctenizidae)	NA	Pertel et al. (2010)
Dendrobatidae				
Ameerega flavopicta (Lutz, 1925)	NA	*Ancylometes* sp. (Ctenidae)	NA	Costa et al. (2006)
Ameerega flavopicta	NA	*Nhandu cerradensis* Bertani, 2001 (Theraphosidae)	NA	Costa et al. (2006)
Ameerega flavopicta	NA	*Phoneutria nigriventer* (Ctenidae)	NA	Costa et al. (2006)
Ameerega flavopicta	NA	*Phoneutria nigriventer* (Ctenidae)	NA	Costa et al. (2006)
Ameerega trivittata (Spix, 1824)	NA	*Ancylometes rufus* (Ctenidae)	NA	

Table 1 (continued)

Anuran species	SVL (mm)	Spiders	Size (mm)	Reference source
				Ramos-Torres and Caicedo-Moncada (2019)
Dendrobates auratus (Girard, 1855)	6.00*	*Sericopelma rubronitens* (Theraphosidae)	45.00*	Summers (1999)
Dendrobates auratus	6.00*	*Diplura* sp. (Dipluridae)	NA	Vollrath (1978)
Ranitomeya reticulatus (Boulenger, 1884)	NA	Unidentified spider	NA	Acosta et al. (2013)
Eleutherodactylidae				
Eleutherodactylus coqui Thomas, 1966	NA	Corinnidae (Unidentified species)	NA	Daza et al. (2008)
Eleutherodactylus cuneatus (Cope, 1862)	10.00	*Ohvida vernalis* (Bryant, 1940) (Ctenidae)	16.30	Fong et al. (2012)
Hylidae				
Aplastodiscus arildae (Cruz and Peixoto, 1987)	35.60	*Trechaleoides biocellata* (Trechaleidae)	NA	Zina and Gonzaga (2006)
Boana albopunctata (Spix, 1824)	48.00*	*Aglaoctenus lagotis* (Lycosidae)	16.00*	Present study
Boana albopunctata	48.00*	*Phoneutria nigriventer* (Ctenidae)	NA	Costa et al. (2006)
Boana bischoffi (Boulenger, 1887)	NA	*Phoneutria nigriventer* (Ctenidae)	NA	Foerster et al. (2017)
Boana crepitans (Wied, 1824)	NA	*Trechalea* sp. (Trechaleidae)	NA	Hernández-Cuadrado and Bernal (2009)
Boana dentei (Bokermann, 1967)	NA	*Ancylometes rufus* (Ctenidae)	NA	Figueiredo et al. (2020)
Boana multifasciata (Gunther, 1859)	NA	*Phoneutria nigriventer* (Ctenidae)	NA	Costa et al. (2006)
Boana pulchella (Duméril and Bibron, 1841)	NA	*Lycosa erythrognata* (Lycosidae)	NA	Villanova et al. (2015)
Boana pulchella	NA	Lycosidae (Unidentified specie)	NA	Villanova et al. (2015)
Boana raniceps (Cope, 1862)	70.00*	*Avicularia* sp. (Theraphosidae)	NA	Present study
Boana sp.	NA	Ctenidae (Unidentified species)	NA	Von May et al. (2019)
Bokermannohyla sapiranga Brandão, Magalhães, Garda, Campos, Sebben and Maciel, 2012	NA	*Ancylometes concolor* (Perty, 1833) (Ctenidae)	NA	Eterovick and Brandão (2001)
Dendropsophus branneri (Cochran, 1948)	14.80*	*Thaumasia* sp. (Pisauridae)	NA	Baracho et al. (2014)
Dendropsophus branneri	14.80*	*Ctenus* sp. (Ctenidae)	NA	Lira et al. (2020)
Dendropsophus branneri	14.80*	*Trichonephila clavipes* (Araneidae)	25.00*	Souza et al. (2019)
Dendropsophus brevifons (Duellman and Crump, 1974)	NA	*Ancylometes rufus* (Ctenidae)	NA	Pinto and Costa-Campos (2017)
Dendropsophus ebraccatus (Cope, 1874)	NA	Ctenidae (Unidentified species)	NA	Donnelly and Guyer (1994)
Dendropsophu elegans (Wied, 1824)	30.00	*Ancylometes* sp. (Ctenidae)	21.00	Serafim et al. (2007)
Dendropsophus elegans	30.47	*Phoneutria nigriventer* (Ctenidae)	29.33	Santana et al. (2009)
Dendropsophus haddadi (Bastos and Pombal, 1996)	NA	*Parawixia kochi* (Taczanowski, 1873) (Araneidae)	NA	Sena and Solé (2019)
Dendropsophus leali (Bokermann, 1964)	NA	*Phoneutria sp.* (Ctenidae)	NA	Von May et al. (2019)
Dendropsophus leucophyllatus (Beireis, 1783)	NA	*Ancylometes* sp. (Ctenidae)	NA	Jansen and Schulze (2008)
Dendropsophus melanargyreus (Cope, 1887)	40.9	*Ancylometes rufus* (Ctenidae)	21.50	Moura and Azevedo (2011)
Dendropsophus melanargyreus	35.00*	*Ancylometes concolor* (Ctenidae)	32.00*	Fadel et al. (2019)
Dendropsophus minutus (Peters, 1872)	NA	*Dolomedes* sp. (Pisauridae)	NA	Bastos et al. (1994)
Dendropsophus minutus	25.00	*Ancylometes sp.* (Ctenidae)	31.10	Bernarde et al. (1999)
Dendropsophus minutus	22.00	*Ancylometes rufus* (Ctenidae)	26.01	Menin et al. (2005)
Dendropsophus minutus	24.50	*Ancylometes rufus* (Ctenidae)	31.00	Menin et al. (2005)
Dendropsophus minutus	NA	*Ancylometes concolor* (Ctenidae)	NA	Bocchiglieri et al. (2010)
Dendropsophus minutus	NA	*Aglaoctenus oblongus* (Koch, 1847) (Lycosidae)	NA	Abegg et al. (2014)
Dendropsophus minutus	19.35	*Thaumasia velox* Simon, 1898 (Pisauridae)	12.02	Bovo et al. (2014)
Dendropsophus minutus	24.00	*Parawixia* sp. (Araneidae)	23.00	Moura et al. (2019)
Dendropsophus minutus	NA	*Thaumasia* sp. (Pisauridae)	25.60	Moura et al. (2019)

Table 1 (continued)

Anuran species	SVL (mm)	Spiders	Size (mm)	Reference source
Dendropsophus microcephalus (Cope, 1886)	NA	*Cupiennius salei* (Keyserling, 1877) (Trechaleidae)	NA	Ríos-Rodas et al. (2016)
Dendropsophus microps (Peters, 1872)	18.09	*Thaumasia velox* (Pisauridae)	16.63	Bovo et al. (2014)
Dendropsophus nanus (Boulenger, 1889)	10.00	*Thaumasia* sp. (Pisauridae)	12.00	Pramuk and Alamillo (2002)
Dendropsophus pseudomeridianus (Cruz, Caramaschi and Dias, 2000)	NA	*Hogna* sp. (Lycosidae)	6.40	Folly et al. (2014)
Dendropsophus sanborni (Schmidt, 1944)	18.30	*Diapontia uruguayensis* Keyserling, 1877 (Lycosidae)	9.50	Del-Grande and Moura (1997)
Dendropsophus sarayacuensis (Shreve, 1935)	15.00	*Ancylometes rufus* (Ctenidae)	9.32	Rodrigues and Arruda (2007)
Dendropsophus werneri (Cochran, 1952)	NA	Lycosidae (Unidentified specie)	NA	Oliveira et al. (2010)
Duellmanohyla rufiocolis (Taylor, 1952)	NA	*Cupiennius coccineus* (Trechaleidae)	NA	Folt and Lapinski (2017)
Itapotihyla langsdorffi (Duméril and Bibron, 1841)	13.90	*Thaumasia* sp. (Pisauridae)	1.77	Luiz et al. (2013)
Osteocephalus leprieurii (Duméril and Bibron, 1841)	42.00	*Ancylometes rufus* (Ctenidae)	35.00	Almeida et al. (2020)
Osteocephalus leprieurii	28.00	*Ancylometes rufus* (Ctenidae)	20.00	Almeida et al. (2020)
Osteocephalus taurinus Steindachner, 1862	90.00*	Pisauridae (Unidentified species)	18.00	Costa-Pereira et al. (2010)
Osteocephalus taurinus	15.00	*Neoctenus* sp. (Ctenidae)	40.00	Costa-Pereira et al. (2010)
Ololygon alcatraz (Lutz, 1973)	23.80	*Oligoctenus medius* (Ctenidae)	NA	Brasileiro and Oyamaguchi (2006)
Ololygon aromothyella (Faivovich, 2005)	17.80	*Thaumasia velox* (Pisauridae)	7.50	Machado and Lipinski (2014)
Ololygon littoralis (Pombal and Gordo, 1991)	NA	*Thaumasia velox* (Pisauridae)	NA	Muscat et al. (2014)
Ololygon littoralis	NA	*Eriophora fuliginea* (Koch, 1838) (Araneidae)	NA	Muscat et al. (2014)
Scinax alter (Lutz, 1973)	14.00	*Thaumasia velox* (Pisauridae)	13.30	Marra et al. (2003)
Scinax alter	27.30	*Ancylometes rufus* (Ctenidae)	23.00	Prado and Borgo (2003)
Scinax alter	11.50	*Thaumasia* sp. (Pisauridae)	10.20	Pinto-Silva and Neuhaus (2018)
Scinax crospedospilus (Lutz, 1925)	49.00*	*Phoneutria nigriventer* (Ctenidae)	30.00	Pacheco et al. (2016)
Scinax elaeochroa (Cope, 1875)	NA	Ctenidae (Unidentified species)	NA	Donelly and Guyer (1994)
Scinax elaeochra	NA	Ctenidae (Unidentified species)	NA	Donelly and Guyer (1994)
Scinax garbei (Miranda-Ribeiro, 1926)	33.20	*Ctenus* sp. (Ctenidae)	24.10	Salas et al. (2019)
Scinax nebulosus (Spix, 1824)	NA	*Ancylometes rufus* (Ctenidae)	NA	Figueiredo et al. (2020)
Scinax ruber (Laurenti, 1768)	NA	*Ancylometes rufus* (Ctenidae)	NA	Costa-Campos et al. (2010)
Scinax ruber	NA	*Thaumasia* sp. (Pisauridae)	NA	Arrivillaga et al. (2019)
Scinax ruber	NA	*Ancylometes rufus* (Ctenidae)	NA	Figueiredo et al. (2020)
Scinax similis (Cochran, 1952)	40.70	*Eriophora fuliginea* (Araneidae)	25.00	Kirchmeyer et al. (2017)
Smilisca sordida (Peters, 1863)	41.00	*Ancylometes bogotensis* (Ctenidae)	21.00	Dehling (2007)
Tlalocohyla loquax (Gaige and Stuart, 1934)	NA	*Cupiennius sp.* (Trechaleidae)	NA	Ugarte and Briggs (2007)
Trachycephalus typhonius (Linnaeus, 1758)	NA	*Dolomedes* sp. (Pisauridae)	NA	Schulze and Jansen (2010)
Hylodidae				
Crossodactylus schmidti Gallardo, 1961	NA	*Phoneutria nigriventer* (Ctenidae)	NA	Caldart et al. (2011)
Hylodes phyllodes Heyer and Cocroft, 1986	17.20	*Trechalea keyserlingi* Cambridge, 1903 (Trechaleidae)	13.80	Schiesari et al. (1995)
Leptodactylidae				
Adenomera andreae (Muller, 1923)	24.00	*Ancylometes rufus* (Ctenidae)	30.00	Menin et al. (2005)
Adenomera andreae	20.90	*Ctenus villasboasi* Mello-Leitão, 1949 (Ctenidae)	18.50	Menin et al. (2005)
Adenomera andreae	11.50	*Ctenus* sp. (Ctenidae)	8.00	Menin et al. (2005)
Adenomera hylaedactyla (Cope, 1868)	16.00*	*Avicularia* sp. (Theraphosidae)	NA	Tavares-Pinheiro et al. (2019)
Adenomera marmorata Steindachner, 1867	15.90		16.20	Barbo et al. (2009)

Table 1 (continued)

Anuran species	SVL (mm)	Spiders	Size (mm)	Reference source
		Ctenus medius Keyserling, 1891 (Ctenidae)		
Engystomops pustulosus (Cope, 1864)	NA	*Trechalea* sp. (Trechaleidae)	NA	Hernández-Cuadrado and Bernal (2009)
Engystomops pustulosus	NA	Ctenidae (Unidentified species)	NA	Carmona et al. (2017)
Leptodactylus didymus Heyer, García-Lopez and Cardoso, 1996	NA	Ctenidae (Unidentified species)	NA	Von May et al. (2019)
Leptodactylus fuscus (Schneider, 1799)	NA	*Ancylometes concolor* (Ctenidae)	NA	Bueno-Villafañe et al. (2018)
Leptodactylus fragilis (Brocchi, 1877)	NA	*Lycosa* sp. (Lycosidae)	NA	Espinoza-Pérnia and Infante-Rivero (2017)
Leptodactylus kudseni	90.00	*Theraphosa blondi* (Theraphosidae)	80.00*	Boistel and Pauwels (2002)
Pseudopaludicola mystacalis (Cope, 1887)	NA	*Ancylometes* sp. (Ctenidae)	NA	Costa and Nomura (2014)
Pseudopaludicola falcipes (Hensel, 1867)	11.10	*Lycosa thorelli* (Keyserling, 1877) (Lycosidae)	13.00	Kacevas et al. (2019)
Pseudopaludicola saltica (Cope, 1887)	14.03	Lycosidae (Unidentified specie)	30.00	Assis et al. (2018)
Pseudopaludicola pocoto Magalhães, Loebmann, Kokobum, Haddad and Garda 2014	NA	*Ancylometes rufus* (Ctenidae)	NA	Silva et al. (2015)
Physalaemus camacan Pimenta, Cruz and Silvano, 2005	NA	*Ctenus rectipes* Pickard-Cambridge, 1897 (Ctenidae)	NA	Mira-Mendes et al. (2017)
Physalaemus cuvieri Fitzinger, 1826	30.00*	*Ancylometes* sp. (Ctenidae)	NA	Maffei et al. (2010)
Physalaemus olfersii (Lichtenstein and Martens, 1856)	NA	*Phoneutria nigriventer* (Ctenidae)	NA	Pedrozo et al. (2017)
Engystomops pustulosus (Cope, 1864)	30.00*	*Sericopelma rubronitens* (Theraphosidae)	45.00*	Gray and Green (1999)
Physalaemus sp.	NA	*Ancylometes* sp. (Ctenidae)	NA	Present study
Microhylidae				
Elachistocleis panamensis (Dunn, Trapido and Evans, 1948)	NA	*Ancylometes bogotensis* (Ctenidae)	NA	Salcedo-Rivera et al. (2018)
Hamptophryne boliviana (Parker, 1927)	NA	*Phoneutria* sp. (Ctenidae)	NA	Von May et al. (2019)
Hamptophryne boliviana	NA	*Pamphobeteus* sp. (Theraphosidae)	NA	Von May et al. (2019)
Phyllomedusidae				
Pithecopus nordestinus (Caramaschi, 2006)	NA	*Thaumasia* sp. (Pisauridae)	NA	Santos-Silva et al. (2013)
Ranidae				
Lithobates warszewitschii (Schmidt, 1857)	26.00	*Kiekie curvipes* (Keyserling, 1881) (Ctenidae)	NA	Folt and Lapinski (2017)
Lithobates warszewitschii	NA	*Kiekie sinuatipes* (Pickard-Cambridge, 1897) (Ctenidae)	NA	Folt and Lapinski (2017)
Unidentified family, genus and species				
Tadpole	NA	*Thaumasia sp.* (Pisauridae)	NA	Von May et al. (2019)
"Tree frog"	NA	*Eriophora edax* (Blackwall, 1863) (Araneidae)	NA	Greenstone (1984)
"Sapos y ranas" (en: toads and frogs)	NA	*Linothele* sp. (Dipluridae)	NA	Paz (1988)

Size in millimeters (mm). SVL: snout-vent length; (*): adult mean species size; NA: average genera size value not available

Theraphosid spiders (Fukushima and Bertani 2017). Although there is another record of predation of an amphibian by an *Avicularia* species (see Tavares-Pinheiro et al. 2019), our record is the first involving a large frog species, such as *Boana raniceps*. This predation may be related to the arboreal habits of those species, along with the ambush foraging present in the Aviculariinae subfamily (Foelix 2011). The genus *Ctenus* Walckenaer, 1805 is composed of medium-sized terrestrial spiders, that can be both ambush and active hunters, usually associated with forest and aquatic environments (Motta 2014). Those habits could have led to opportunistic encounters with *Ischnocnema parva* and *Barycholos ternetzi*, also leaf litter forest dwellers (Martins et al. 2010; Santoro and Brandão 2014). Although there have been other records of predations on amphibians by the *Ctenus* genus (Table 1), this is the first record of predation on those species. The ctenid genus

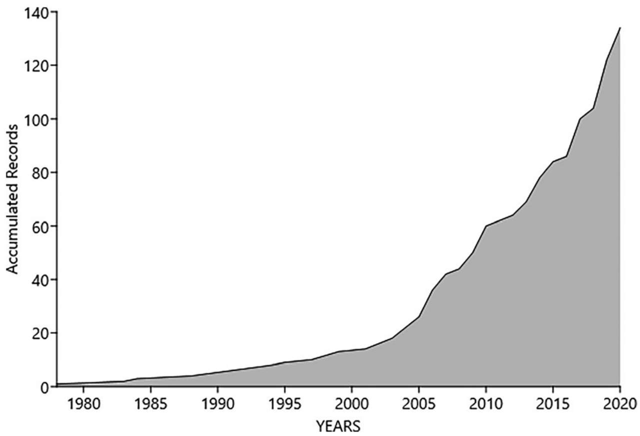

Fig. 2 Accumulated records of predatory events published between 1978 and 2020

Ancylometes, involved in most of the records, consists of medium-large opportunistic spider species, strongly related to humid habitats (Höfer and Brescovit 2000), which might explain the higher number of events recorded involving this spider, including two of our reports.

Despite the stunning spider diversity in the Neotropical region, with more than 11,280 species (Brescovit et al. 2011), only 63 spider species have records of predation in anurans, including our six new records (Table 1). We expanded this list with two species (*A. lagotis* and *C.* cf. *ornatus*), which have never been recorded to be anuran predators. There were two records of predation on large anuran species found in the literature, and such events seem to be infrequently detected. Theraphosid spiders are known sit-and-wait predators (Foelix 2011), and large-sized species such as *T. blondi* could be eventual predators of large frog species. Similarly, anurans are profitable prey for large-sized spiders, providing the energy necessary for survival, growth, and reproduction (see Uetz 1992). Although in a few events the spider was bigger than the frog (e.g. *Dendrobates auratus* vs. *Sericopelma rubronitens*),

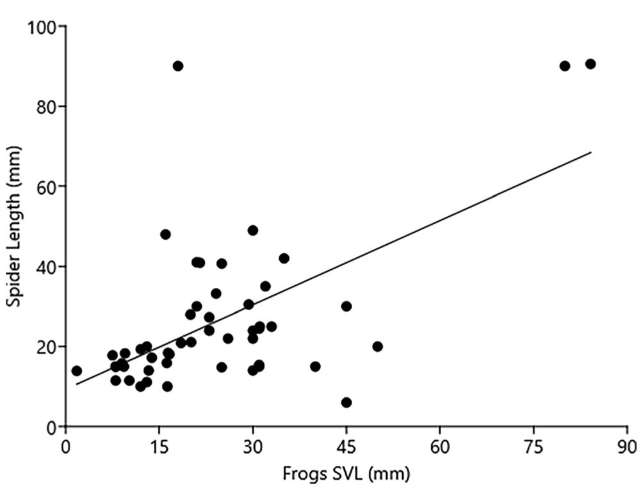

Fig. 3 Size relationships between spider predators and anuran prey, based on literature data ($N = 51$; $y = 0.7x + 9.34$; $r2 = 0.348$; $p = 0.0007$)

we reported the opposite in almost all predation reports. This can be explained by the fact that spiders do not need to swallow their prey, and the presence of venom is a determining factor in defining prey-predator size relationships (McCormick and Polis 1982), having spiders the ability to subjugate larger preys. Spider venom, which is effective against amphibians, especially in ctenid spiders (Foelix 2011), along with the large size of some species, make these arachnids a major predator of vertebrates (Valdez 2020). We suggest that feeding on vertebrates may be a major determinant of venom evolution in spiders (Garb et al. 2004; Bucaretchi et al. 2018; Nyffeler and Vetter 2018; Valenzuela-Rojas et al. 2019), selecting more toxic and effective venoms for such class of prey (see Garb and Hayashi 2013). Not surprisingly, most of the spider genera involved in serious human envenomation often prey on vertebrates (McCormick and Polis 1982; Saucier 2004; Haddad et al. 2012, 2015).

Anurans are the largest group of vertebrate prey to arthropod predators (Valdez 2020), and spiders are the most important arthropod predators of adult anurans (Toledo 2005). However, we found a wide overlap on frog families' use by spider families, highlighting the opportunistic and non-discriminatory nature of spiders as frog predators Some families of spiders are opportunistic and generalist predators (Rego et al. 2005), explaining the large overlap on preyed frog families, despite their differences in hunting strategies and anuran size variation. As expected, the observed predator-prey relationship is also determined by the size (Menin et al. 2005; Lima et al. 2006; Pertel et al. 2010; Gaiarsa et al. 2012). Spiders probably can evaluate the frog size, avoiding large-sized species, which may be potential predators (Brodie III and Brodie 1999) or hard-to-manage prey items, thus producing the relationship on predator and prey sizes (Fig. 5). However, there is a high prevalence of predatory events on small anurans (15–25 mm SVL), a finding that may be related to the high abundance of smaller frogs, especially Hylidae and Leptodactylidae (Giaretta et al. 2008; Araújo and Almeida-Santos 2013). Therefore, the size effect of prey and predator for spiders and frogs is determined by a trade-off between the spider's ability to handling larger prey and the opportunity to capture smaller (and less profitable) frogs.

Encounters between frogs and their predators are more frequent during the breeding season (Toledo 2003; Pacheco et al. 2016), also representing the period with the highest availability of metamorphic anurans in the environment (Barreto and Moreira 1996). The predation on froglets may be related to the fact that they are more easily preyed on due to a lack of developmental accommodations for aquatic and terrestrial environments (Toledo 2003; Fadel et al. 2019), being the most vulnerable life-stage for amphibians (Johansson et al. 2010). Immature amphibians are also vulnerable due to their smaller size, which is a disadvantage against larger cursorial spiders (McCormick and Polis 1982). The spatial distribution of

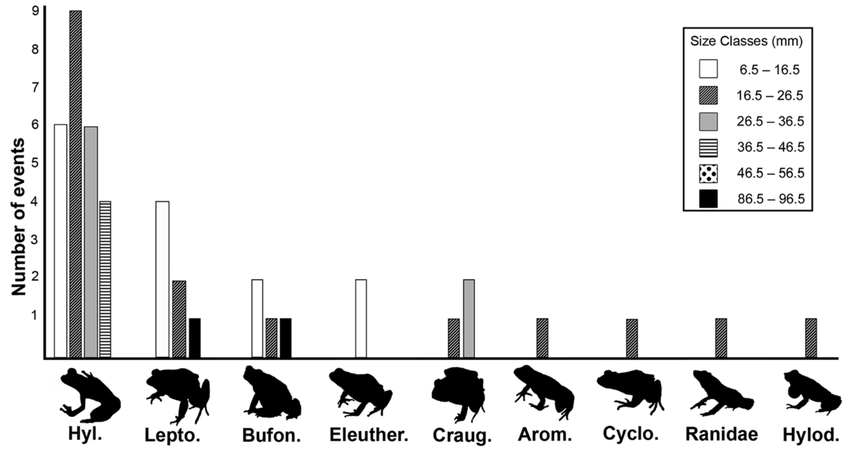

Fig. 4 Number of predation events per family by size classes of preyed anurans recorded by the literature review and our new records. Different patterns indicate different size classes of the frogs (Abbreviations are Hyl. =Hylidae, Lepto. = Leptodactylidae, Bufon. = Bufonidae, Eleuther. = Eleutherodactylidae, Craug. = Craugastoridae, Arom. = Aromobatidae, Cyclo. = Cycloramphidae, Hylod. = Hylodidae)

predator spiders and anuran prey (adult and metamorphic) is coincidental along the edge of aquatic environments, inducing predator response against a relatively mobile prey (Sih 1984), or in this scenario, a froglet shifting to more terrestrial environments. Since terrestrial wandering spiders are sit-and-wait predators that locate prey mainly by their movements (Foelix 2011), the stillness of froglets (and adult frogs; see Cooper et al. 2008) can be an effective strategy for avoiding spider predation in a very sensitive developmental stage.

Anuran predation by spiders in Neotropical ecosystems is common (Valdez 2020) and maybe a relevant source of mortality for several anuran species, especially during recruitment. The growing in published anecdotal reports on frog predation by spiders can be useful for further studies (e.g. Menin et al. 2005; Toledo 2005). However, most of the reported events lack crucial pieces of information, such as predator and prey identification to the lowest possible taxonomic level, their sizes, predatory and antipredatory strategies used, time for prey capture and ingestion, anuran stage, the hour and date of the reported event, along with habitat characteristics. We suggest that most of these informations should be available in future reports, allowing for further insights and predictions about this ecological relationship on Neotropical spiders and frogs.

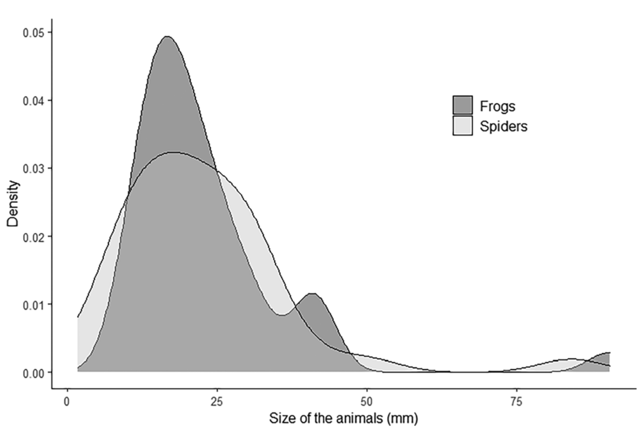

Fig. 5 Kernel density graph to estimate the unknown population of frog and spider size distributions from literature data. Higher densities represent a higher number of publications involving the size of the animals

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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Consent to participate Not applicable.

Consent for publication Not applicable.

Code availability Not applicable.

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