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REVIEW

Spiders as frog-eaters: a global perspective

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Abstract. In this paper, 374 incidents of frog predation by spiders are reported based on a comprehensive global literature and social media survey. Frog-catching spiders have been documented from all continents except for Antarctica (>80% of the incidents occurring in the warmer areas between latitude 30° N and 30° S). Frog predation by spiders has been most frequently documented in the Neotropics, with particular concentration in the Central American and Amazon rain forests and the Brazilian Atlantic forest. The captured frogs are predominantly small-sized with an average body length of 2.76 ± 0.13 cm (usually ≈0.2–3.8 g body mass). All stages of the frogs' life cycle (eggs/embryos, hatchlings, tadpoles, emerging metamorphs, immature post-metamorphs, adults) are vulnerable to spider predation. The majority (85%) of the 374 reported incidents of frog predation were attributable to web-less hunting spiders (in particular from the superfamilies Ctenoidea and Lycosoidea) which kill frogs by injection of powerful neurotoxins. The frog-catching spiders are predominantly nocturnal with an average body length of 2.24 ± 0.12 cm (usually ≈0.1–2.7 g body mass). Altogether >200 frog species from 32 families (including several species of bitter tasting dart-poison frogs) have been documented to be hunted by >100 spider species from 22 families. Our finding that such a high diversity of spider taxa is utilizing such a high variety of frog taxa as prey is novel. The utilization of frogs as supplementary food increases the spiders' food supply (i.e., large diet breadth), and this is presumed to enhance their chance of survival. Studies from Australia and South America indicate that frogs might be a substantial component in the diet of some mygalomorph spiders (i.e., families Atracidae, Idiopidae, and Theraphosidae). Many more quantitative investigations on the natural diets of tropical spiders are needed before reliable conclusions on the importance of frogs as spider food can be drawn.

Keywords: Araneae, Anura, predation, dart-poison frogs, nutritional importance, survival capability

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1. INTRODUCTION

Spiders are among the most common and abundant predators in terrestrial ecosystems (Turnbull 1973; Coddington & Levi 1991; Nyffeler & Sunderland 2003). With >48,300 described species, these animals exhibit an enormous diversity of life styles and foraging strategies (Nyffeler & Birkhofer 2017; World Spider Catalog 2019). For a long time, spiders had been believed to depend almost exclusively on live insects or other small arthropods for food (Nyffeler 1999). More recently, it has been shown that the spiders' natural diets are actually broader than previously thought, including "odd foods" such as earthworms, onychophorans, polychaete worms, slugs, snails, amphipods, shrimps, crayfish, freshwater crabs, and various types of plant materials (Nyffeler & Symondson 2001; Nyffeler et al. 2016, 2017b). Spiders also capture a variety of small vertebrates, including birds, bats, mice, deer mice, voles, shrews, rats, mouse lemurs, mouse opossums, pygmy possums, fish, snakes, lizards, newts, salamanders, lungless salamanders, mole salamanders, caecilians, frogs, and toads (e.g., Raven 1990; Menin et al. 2005; Toledo 2005; Brooks 2012; Nyffeler & Knörnschild 2013; Nyffeler & Pusey 2014; Nyffeler & Vetter 2018; Martin 2019; von May et al. 2019).

A large number of incidents of frog predation by spiders has been reported in the scientific literature and in the social media. Menin et al. (2005) and Toledo (2005) published reviews on frog-eating spiders after surveying the scientific literature accessible from 1940–2004. Toledo (2005), who conducted an extensive literature survey biased towards the Neotropics, concluded that spiders from ten different families preyed on frogs representing ten families. Several reports published prior to 2005 had been overlooked in these two reviews. Moreover, many new reports on frog predation by spiders became known from 2005 onwards (e.g., Ahmed et al. 2017; Deluna & Montoya 2017; Espinoza-Pernía & Infante-Rivero 2017; Foerster et al. 2017; Folt & Lapinski 2017; Garcia-Vinalay & Pineda 2017; Kirchmeyer et al. 2017; Mira-Mendes et al. 2017; Nyffeler et al. 2017a; Pedrozo et al. 2017; Pinto & Costa-Campos 2017; Poo et al. 2017; Yetman et al. 2017; Bueno-Villafañe et al. 2018; Giri et al. 2018; Portik et al. 2018; Salcedo-Rivera et al. 2018; Baba et al. 2019; Babangenge et al. 2019; Delia et al. 2019; Landgref Filho et al. 2019; Salas et al. 2019; Sena & Solé 2019; von May et al. 2019). To close this gap, a comprehensive global survey on frog-eating spiders was conducted taking into account sources from the scientific literature and the social media accessible from 1883–2019, and the insights from this research are presented here.

2. METHODS

2.1 Data collection.—Published reports on frog predation by spiders were searched for using Thomson-Reuters database, Elsevier's Scopus database, Google Search, Google Scholar, Google Books, and Google Pictures as well as ProQuest Dissertations and Theses (compare Nyffeler et al. 2017c). Social media sites were searched as well. Books and scientific journals not included in the large databases were hand-searched. A total of 374 reports of predation (or predation attempts) on frogs by spiders were found, 80% of which had previously been published in the scientific literature (see Supplementary material, online at http://dx.doi.org/10.1636/JoA-S-19-051.s1). The remaining 20% were found on social media sites (e.g., Scientific American, National Geographic, BBC, YouTube, Project Noah, Panama Birds & Wildlife etc.; see Supplementary material, online at http://dx.doi.org/10.1636/JoA-S-19-051.s1) or provided to us by scientists/photographers as personal communications. Three hundred and thirty-seven of the 374 records (90%) refer to observational natural history studies in the field; the remaining 37 records are based on laboratory trials or field experimental studies. In cases where it was stated that a certain type of predation event had been witnessed several times (without providing an exact number; Hernández-Cuadrado & Bernal 2009), we counted this type of predation event 3 x as a proxy to the unknown true number. In this paper, the Neotropic realm is understood as the combined area of Mexico, Central America, South America, and the Caribbean, whereas all information referring to Florida is included in the USA.

2.2 Identification of unidentified spiders and frogs depicted in photos.—For 194 of the 374 reports (= 52%), the predation events were evidenced by means of photos and/or videos. For some photos or videos which depicted unidentified spiders and/or frogs, those were identified on our behalf by established spider and anuran taxonomists to the lowest taxon possible. Spiders were identified by A. Brescovit, A. Dippenaar-Schoeman, G.B. Edwards, H. Höfer, K. Kissane, F. Pérez-Miles, R. Raven, A. Santos, E. L. Cruz da Silva, and R. West, while frog identifications were provided by A. Amey and K. L. Krysko. R. Altig identified two tadpoles from Ecuador based on photos. Frog and spider nomenclatures are based on Frost's (2019) "Amphibian Species of the World" and the "World Spider Catalog 2019". For reasons of simplicity all reported anurans (including the bufonids) are termed in this paper as "frogs". In 330 instances, the identity of the reported frog victims is known at least at family level, whereas 44 frog victims remain unidentified or doubtful. Contrary to the "World Spider Catalog 2019", we placed the genus *Trichonephila* in the family Nephilidae (*sensu* Kuntner et al. 2019).

Body length of spiders is understood as the length of the cephalothorax + abdomen (without legs). Frog body length is defined as snout-vent length of post-metamorphs and total body length (snout-vent length + tail length) of tadpoles. Whenever possible – that is, in most cases – body length data were taken from the papers. In very few cases, where exclusively leg span data were available for spiders, those were converted to body length by multiplication of the leg span by 0.34 (Pisauridae and Ctenidae) and 0.20 (Trechaleidae), respectively; the conversion factors had been determined after making measurements on spider habitus photos retrieved from Google Pictures.

Based on frog body length information corresponding frog body mass values have been roughly estimated based on published frog length/body mass ratios (see Nyffeler et al. 2017a) if frog body mass was not provided in the published predation accounts. The frog body mass data are biased towards araneomorph spiders due to the fact that in 56 of the 58 documented incidents of frog predation by mygalomorphs body mass data were unavailable and could therefore not be included in the calculation of average frog body mass.

2.3 Statistical methods.—The Mann-Whitney *U* test (see MacFarland & Yates 2016) was applied to examine whether mean frog body length ($n = 118$) differed statistically significantly from mean spider body length ($n = 96$). Prior to that, it was shown by means of normal probability plots that frog length data and spider body length data both were not normally distributed. Mean values are followed by Standard Errors (± SE).

3. RESULTS

3.1 Which spider species are engaged in frog predation?—A total of 106 spider species have been reported to prey on frogs under natural conditions, and ten additional species have been documented to kill and eat frogs in captivity (Table 1 and Appendix 1). According to our survey, frogs were captured to a large extent by nocturnal spiders (>80% of frog predation

Table 1.—Spider families engaged in frog predation (based on 374 incidents reported in the scientific literature or in the social media). Evidence based on field observations, except for Dictynidae.

Taxon#	Spider family	Number of species within family	Number of predation events	Source
01	Actinopodidae	2	2	Gordh & Headrick 2011; Australian Museum 2018
02	Anyphaenidae	1	3	Rojas-Morales & Escobar-Lasso 2013; Delia et al. 2019
03	Araneidae	8	20	Greenstone 1984; Lockley 1990; Muscat et al. 2014; Folt & Lapinski 2017; Kirchmeyer et al. 2017; and others
04	Atracidae	3	3	Rainbow & Pulleine 1918; McKeown 1952; Brunet 1998
05	Barychelidae	1	1	Brunet 1998
06	Clubionidae	1	1	Almeida-Reinoso & Coloma 2012
07	Corinnidae	1	1	Daza et al. 2008
08	Ctenidae	18	89	Menin et al. 2005; Folt & Lapinski 2017; Babangenge et al. 2019; von May et al. 2019; and others
09	Ctenizidae	1	1	Pertel et al. 2010
10	Dictynidae[A,B]	1	1	Bristowe 1958
11	Dipluridae	2	3	Vollrath 1978; Paz 1988 / Paz & Raven 1990
12	Gnaphosidae	1	1	Gopi Sundar 1998
13	Idiopidae	2	14	Butler & Main 1959; Main 1996
14	Lycosidae[C]	17	40	Sharma & Sharma 1977; Raven 1990; Raven 2000; Almeida et al. 2010; DeVore & Maerz 2014; and others
15	Miturgidae	1	1	Robert Raven, pers. comm.
16	Nephilidae[D]	2	5	Gudger 1925; Ganong & Folt 2015; and others
17	Pisauridae	20	91	Jeffery et al. 2004; Vonesh 2005; Bovo et al. 2014; Baba et al. 2019; Babangenge et al. 2019
18	Salticidae	2	10	O'Neill & Boughton 1996; Ahmed et al. 2017; Nyffeler et al. 2017a; and others
19	Sparassidae[E]	5	11	Formanowicz et al. 1981; Turner 2010; Hamidy et al. 2010; Tanaka 2013; and others
20	Theraphosidae[F]	18	34	McKeown 1952; Main & Main 1956; Summers 1999; Menin et al. 2005; Toledo 2005; and others
21	Theridiidae	2	2	Anderson 2011; and others
22	Trechaleidae	7	33	Zina & Gonzaga 2006; Hernández-Cuadrado & Bernal 2009; Gaiarsa et al. 2012; Folt & Lapinski 2017; and others
–	Unspecified	N/A	7	Acosta et al. 2013; Babangenge et al. 2019; and others
Total		116	374	

[A] *Argyroneta aquatica* observed eating tadpoles in captivity (also see Schmidt 1980; Uzenbaev & Lyabzina 2009)
[B] Placement of *Argyroneta aquatica* in family Dictynidae (World Spider Catalog 2019) – previously placed in Cybaeidae (Platnick 2014)
[C] Three species observed eating frogs in captivity, 14 species observed eating frogs in the field
[D] *Trichonephila* placed in Nephilidae (sensu Kuntner et al. 2019)
[E] One species observed eating frogs in captivity, 4 species observed eating frogs in the field
[F] Five species observed eating frogs in captivity, 13 species observed eating frogs in the field

occurring between 18:00 and 04:00 h). The following 21 families have been documented to be engaged in frog predation under natural conditions: Actinopodidae, Anyphaenidae, Araneidae, Atracidae, Barychelidae, Clubionidae, Corinnidae, Ctenidae, Ctenizidae, Dipluridae, Gnaphosidae, Idiopidae, Lycosidae, Miturgidae, Nephilidae, Pisauridae, Salticidae, Sparassidae, Theraphosidae, Theridiidae, and Trechaleidae (Table 1 and Appendix 1). In addition to this, an aquatic species (the diving bell spider *Argyroneta aquatica*) from the family Dictynidae has been witnessed killing and consuming tadpoles under laboratory conditions (Bristowe 1958; Schmidt 1980). Female and male spiders have been reported feeding on frog prey (Figs. 1a,b, 2f). The frog-eating spiders had an average body length of 2.24 ± 0.12 cm (median $= 2.00$ cm, $n = 96$) as far as body length data were available, which corresponds with an average body mass of ≈ 1 g (range $= 0.1–2.7$ g).

Basically four types of frog-eating spiders can be distinguished based on foraging manner: aerial-web weavers, funnel-web weavers, trapdoor spiders, and cursorial hunters (Appendix 1). Frog predation by aerial-web or funnel-web weavers (9% of the 374 incidents) occurred when frogs hopping from shrub to shrub were intercepted in the strong aerial webs of araneid, nephilid, or theridiid spiders (Figs. 1a,b; Groves & Groves 1978; Greenstone 1984; Lockley 1990; Szymkowiak et al. 2005; Muscat et al. 2014; Folt & Lapinski 2017; Kirchmeyer et al. 2017) or when they accidentially landed on the funnel-webs of atracid or diplurid spiders (Rainbow & Pulleine 1918; McKeown 1952; Vollrath 1978; Paz 1988; Brunet 1998). Frogs seized by trapdoor spiders from four families (i.e., Actinopodidae, Barychelidae, Ctenizidae, and Idiopidae) accounted for 5% of the 374 reported incidents (see Butler & Main 1959; Main 1996; Brunet 1998; Pertel et al. 2010; Gordh & Headrick 2011).

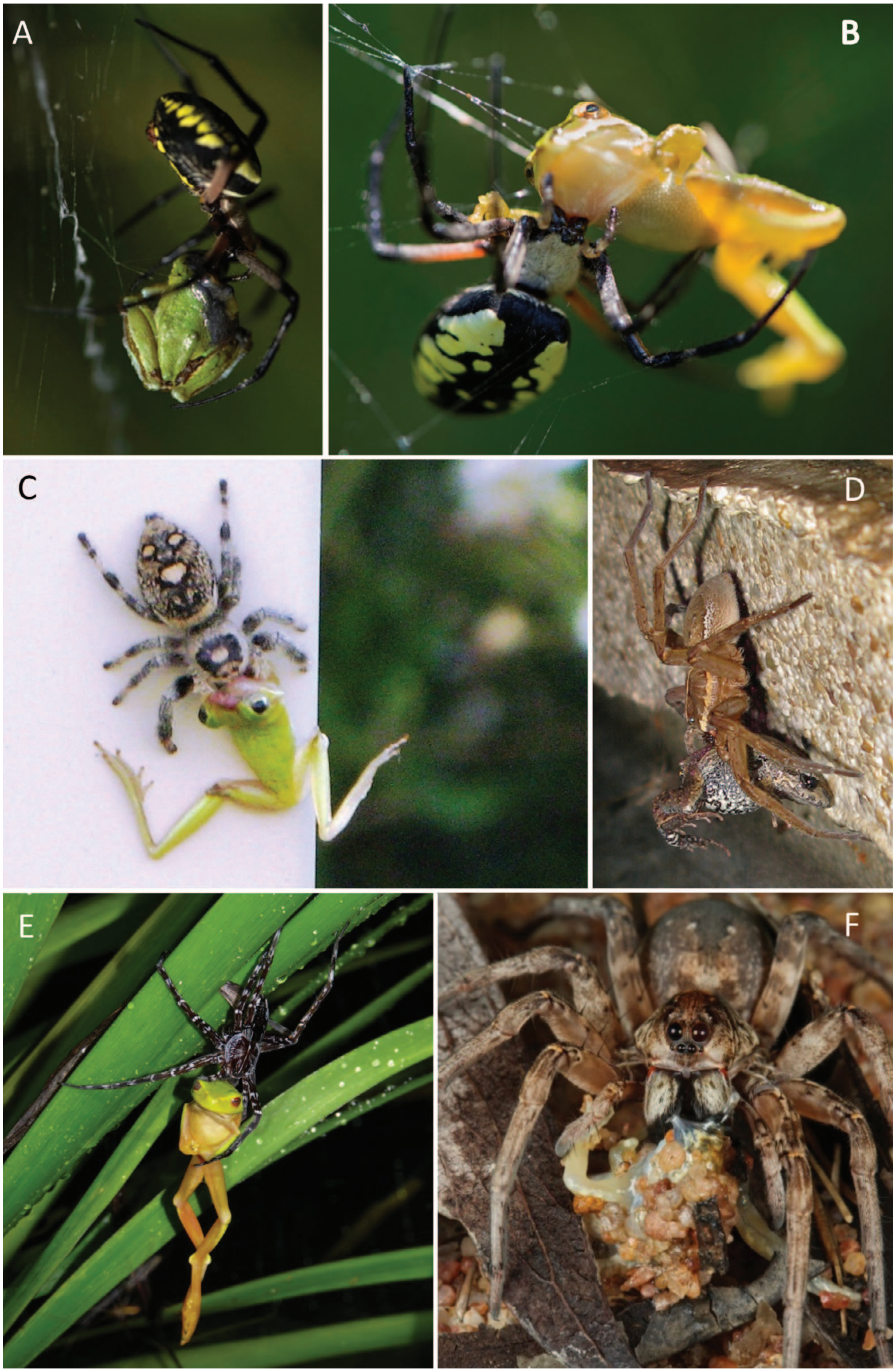

Figure 1.—**a–b** Female *Argiope aurantia* (Araneidae) is wrapping a *Hyliola regilla* frog (Hylidae) in Oregon, USA (photo by Robin Loznak, Oregon). **c** Female *Phidippus regius* (Salticidae) feeding on a Cuban tree frog (*Osteopilus septentrionalis*; Hylidae) in a residential area in Land O' Lakes, Florida (photo by Jeanine DeNisco). **d** Fishing spider (*Dolomedes* sp. – probably *D. facetus*) feeding on *Crinia signifera* (Myobatrachidae) above a swimming pool in Sydney, Australia (photo by Susan Bell, Sydney). **e** *Megadolomedes australianus* (Pisauridae) feeding on a *Litoria gracilenta* in Barratt Creek, Queensland, Australia (photo by Barbara Maslen "Wild Wings & Swampy Things Nature Refuge, Daintree"). **f** Wolf spider (possibly *Tasmanicosa godeffroyi*, Lycosidae) digesting a metamorph *Ranoidea* sp. (Pelodryadidae) in Australia (photo by Nick Volpe, Australia).

The majority of the frog-eating spiders were cursorial hunters (85% of the 374 incidents; Figs. 1c–f, 2a–f) known to capture prey without a web. Wandering spiders (Ctenidae), wolf spiders (Lycosidae), fishing spiders (Pisauridae), and longlegged water spiders (Trechaleidae) are four groups of related web-less hunters in the superfamilies Ctenoidea and Lycosoidea, which particularly frequently hunt frogs (Figs. 1d–f, 2c,d,f). Pisauridae and Ctenidae were the most commonly reported families in this study (respectively 91 and 89 of 374 reported incidents; Table 1). These expert frog hunters were observed to jump on frogs, grab them, and inject them with their potent venoms containing hundreds of different neurotoxins, some of which are specific to vertebrate nervous systems (Duellmann & Trueb 1994; McCormick et al. 1993; Gregio et al. 1998; Cavendish 2003; Behler & Behler 2005; Barbo et al. 2009; Jiang et al. 2013; Nyffeler & Pusey 2014).

It took spider venom ≈1–20 minutes to kill a frog tadpole and ≈1.5–90 minutes to kill a post-metamorphic frog (Del-Grande & Moura 1997; Gopi Sundar 1998; Jeffery et al. 2004; Menin et al. 2005; Dehling 2007; Uzenbaev & Lyabzina 2009; Santos-Silva et al. 2013; Bovo et al. 2014). Some authors stated that a large area of necrotic tissue was immediately visible around the bite site (Blackburn et al. 2002; Serafim et al. 2007; Brunetti 2008), while other researchers observed that frogs quickly developed a hemorrhage-like discoloration in the bitten part of the body (Hayes 1983; Ortega-Andrade et al. 2013; Folt & Lapinski 2017). Jeffery et al. (2004) reported that "the frog lost some green pigmentation and started to become transparent." Shortly after the bite, digestive enzymes released from the spider's mouth began dissolving the victim's tissues outside the spider body (extraintestinal digestion), often supported by squashing movements of the chelicerae, and after a while the spider began imbibing the liquefied prey tissue through its mouth (Fig. 1f). This process of extraintestinal digestion of a frog prey lasted between 0.5–48 hours depending on the spider's hunger level and the size ratio between a spider and its victim (Emerton 1926; Schmidt 1957; Formanowicz et al. 1981; Hawkeswood 2003).

3.2 Which frog species are captured by spiders?—The vast majority of captured frogs had a mean body length of 2.76 ± 0.13 cm (median = 2.40 cm, $n = 118$). Frog body mass usually ranged between ≈0.2–3.8 g based on the available data. The fact that the majority of frog victims was of small size may be explained by the capability of larger frogs to escape by kicking free after having been captured for a brief moment (Toledo et al. 2007). There are exceptions to this rule, especially if large, powerful spiders in the families Ctenidae and Theraphosidae are involved. A large wandering spider (*Phoneutria* sp.) has been reported devouring a bufonid with a body length of ≈6 cm, and a giant tarantula (*Theraphosa blondi*) fed on a bufonid of 9 cm body length (Menin et al. 2005; Silva-Silva et al. 2013).

All stages (eggs/embryos, hatchlings, tadpoles, emerging metamorphs, immature post-metamorphs, adults) of the frogs' life cycle are vulnerable to spider predation (Appendix 2). Most reports referred to the capture of post-metamorphic stages (76.9% of all incidents), whereas predation on metamorphs and tadpoles has been reported in 4.6% and 9.9% of all incidents, respectively. The remaining cases referred to the consumption of eggs/embryos (3.2%), hatchlings (0.3%), and unspecified cases (5.1%) (also see Cabrera-Guzmán et al. 2015; Poo et al. 2017).

Tadpoles, a frog's aquatic larval stages, were captured almost exclusively by semi-aquatic or aquatic spiders (genera *Ancylometes* spp., *Argyroneta aquatica*, *Diapontia uruguayensis*, *Dolomedes* spp., *Megadolomedes australianus*, *Nilus* spp., *Pardosa pseudoannulata*, *Pirata* spp., and *Thaumasia velox*) which live in or near water bodies (Figs. 1d,e, 2f; Rogers 1996; Schulze & Jansen 2010; Santos-Silva et al. 2013; Luiz et al. 2013; Machado & Lipinski 2014; Ahmed et al. 2017). Such spiders have been observed to seize tadpoles as they surface to breathe (Moore & Townsend 1998; McIntyre 1999). Some of the spider species capable of capturing tadpoles are known to occasionally kill and eat small fish (see Nyffeler & Pusey 2014). Spiders as small as 0.65 cm in body length had been witnessed capturing tadpoles (Folly et al. 2014). The aquatic species *Argyroneta aquatica,* previously placed in the family Cybaeidae and now in Dictynidae (see World Spider Catalog 2019), captured tadpoles in the laboratory (Bristowe 1958; Schmidt 1980; Uzenbaev & Lyabzina 2009). Bristowe (1958) stated with regard to this species "….The large adult spiders of half an inch or more can catch and kill tadpoles but after chewing them for a time they usually discard them."

The group of frogs killed and eaten by spiders in the wild encompasses 199 species representing 30 families (i.e., Allophrynidae, Aromobatidae, Arthroleptidae, Brachycephalidae, Bufonidae, Centrolenidae, Craugastoridae, Cycloramphidae, Dendrobatidae, Dicroglossidae, Eleutherodactylidae, Hemiphractidae, Hylidae, Hylodidae, Hyperoliidae, Leptodactylidae, Limnodynastidae, Mantellidae, Microhylidae, Myobatrachidae, Pelodryadidae, Phrynobatrachidae, Phyllomedusidae, Pipidae, Pyxicephalidae, Ranidae, Ranixalidae, Rhacophoridae, Scaphiopodidae, Telmatobiidae; Table 2 and Appendix 2). In addition to this, ten more frog species (among others from the families Ceratobatrachidae and Megophryidae) were killed and consumed by spiders under laboratory conditions. Altogether a total of 209 frog species have been reported to be prey of spiders (see Appendix 2). Thus, 59% of the 54 recognized frog families (see Frost 2019) contain species occasionally captured by spiders. Six families (Hylidae, Leptodactylidae, Bufonidae, Ranidae, Craugastoridae, and Hyperoliidae) accounted for ≈60% of all identified frog victims, with tree frogs (Hylidae) being the most representative family (111 incidents, Table 2). Old World and New World frogs as well were documented to be hunted down by spiders (see Appendix 2).

Schalk & Morales (2012) stated that "Calling male frogs are more conspicuous to a variety of predators than conspecific females at a breeding site" and several researchers who observed spiders hunting vocalizing male frogs came to the conclusion that the predation risk may be higher for male than for female frogs (e.g., Mitchell 1990; Gopi Sundar 1998; Hamidy et al. 2010; Bovo et al. 2014; Pedrozo et al. 2017). Our global survey apparently confirms this; adult male frogs were 4.3 times more frequently reported to be spider victims than adult female frogs.

3.3 Global distribution of frog predation by spiders.—Predation on frogs by spiders has been witnessed in >40 countries; see Supplementary material, online at http://dx.doi.org/10.1636/JoA-S-19-051.s1). Predation on frogs by spiders is

Table 2.—Frog families reported to be victims of spider predation (based on 374 incidents reported in the scientific literature or social media). Evidence based on field observations except for Ceratobatrachidae and Megophryidae.

Taxon#	Frog family	Number of species within family	Number of predation events	Source
01	Allophrynidae	1	1	Jean-Pierre Vacher, pers. comm.; Fig. 2d
02	Aromobatidae	5	5	Menin et al. 2005; de Carvalho et al. 2013; and others
03	Arthroleptidae	1	1	Babangenge et al. 2019
04	Brachycephalidae	1	2	Pontes et al. 2009; and others
05	Bufonidae	15	26	Raven 2000; Menin et al. 2005; White 2015; and others
06	Centrolenidae	7	11	Almeida-Reinoso & Coloma 2012; Folt & Lapinski 2017; Delia et al. 2019; and others
07	Ceratobatrachidae	1	1	Rasalan et al. 2015
08	Craugastoridae	13	17	Ervin et al. 2007; Folt & Lapinski 2017; and others
09	Cycloramphidae	2	2	Pertel et al. 2010; Gaiarsa et al. 2012
10	Dendrobatidae	6	14	Vollrath 1978; Summers 1999; da Costa et al. 2006; Hantak et al. 2016; Acosta et al. 2013; and others
11	Dicroglossidae	1	3	Bhatnagar 1970; Sharma & Sharma 1977
12	Eleutherodactylidae	3	6	Formanowicz et al. 1981; Fong et al. 2012; and others
13	Hemiphractidae	1	1	Morley Read. Online at https://www.shutterstock.com/de/video/clip-27045070-large-wandering-spider-family-ctenidae-feeding-on
14	Hylidae	67	111	Menin et al. 2005; Folt & Lapinski 2017; Kirchmeyer et al. 2017; Nyffeler et al. 2017a; and others
15	Hylodidae	2	2	Schiesari et al. 1995; Caldart et al. 2011
16	Hyperoliidae	13	17	Portik et al. 2018; Babangenge et al. 2019; and others
17	Leptodactylidae	21	31	Menin et al. 2005; Toledo 2005; Barbo et al. 2009; Pedrozo et al. 2017; von May et al. 2019; and others
18	Limnodynastidae	2	3	McKeown 1952; Main & Main 1956
19	Mantellidae	1	1	Mariusz Kluzniak. Online at https://www.gettyimages.ch/detail/foto/madagascar-spider-eating-dart-frog-lizenzfreies-bild/544852871
20	Megophryidae	1	1	Airamé & Sierwald 2000
21	Microhylidae	5	8	Bhatnagar 1970; Menin et al. 2005; von May et al. 2019
22	Myobatrachidae	2	14	Butler & Main 1959; and others
23	Pelodryadidae	8	13	Raven 1990; Valentic 1997; Turner 2010
24	Phrynobatrachidae	1	1	Gudger 1925; Babangenge et al. 2019
25	Phyllomedusidae	4	6	Menin et al. 2005; Santos-Silva et al. 2013
26	Pipidae	3	5	Gudger 1925; Babangenge et al. 2019; and others
27	Pyxicephalidae	3	3	Yetman et al. 2017; Babangenge et al. 2019
28	Ranidae	10	19	Zimmermann & Spence 1989; Folt & Lapinski 2017
29	Ranixalidae	1	1	Ahmed et al. 2017
30	Rhacophoridae	6	6	Tanaka 2013; Sung & Li 2013; Poo et al. 2017
31	Scaphiopodidae	1	1	Farr et al. 2010
32	Telmatobiidae	1	1	Brunetti 2008
–	Unspecified	N/A	40	McKeown 1952; Main 1996; and others
Total		209	374	

a global pattern occurring on all continents except for Antarctica. The vast majority (58%) of reported cases of frog predation by spiders originates from the Neotropics, with particular concentrations in the rain forests of Central and South America and the South American Atlantic forest and to a lower extent in ponds and ravines of the Brazilian Cerrado and Caatinga Biomes, and the Argentinean pampas. There, frog predation had been witnessed on the banks of rivers and streams, near shallow puddles and creeks on the forest floor, on leaf litter of the forest floor, on leaves in the forest understory, and on bromeliads (e.g., Formanowicz et al. 1981; Hayes 1983; Brasileiro & Oyamaguchi 2006; Pazin 2006; Hernández-Cuadrado & Bernal 2009; de Carvalho et al. 2013; Jablonski 2015; Folt & Lapinski 2017; von May et al. 2019). The predominance of reports from this part of the world may reflect that this region is a biodiversity hotspot for both frogs and spiders and harbors a particularly high proportion of the world's frog and spider species (Duellmann 1988; Santos et al. 2017). The many herpetologists and arachnologists from all over the world that conduct field research in the Neotropics increases the likelihood that incidents of frog predation by spiders are detected in that region (see Menin et al. 2005; Toledo 2005; Toledo et al. 2007; Folt & Lapinski 2017).

To a lower extent, incidents of frog predation were also reported from Australia (12% of the total), USA (12%), Africa (8%), Asia (8%), Europe (<2%), and Canada (<1%). Why are occurrences of frog predation by spiders so rare in the colder climates of Central, Western, and Northern Europe and Canada as compared to the warmer climates of the USA and the Neotropics? First, frogs are less abundant in colder climates (Duellmann 1988; Dahl et al. 2009) and accordingly the likelihood of predation on frogs to occur seems to be lower

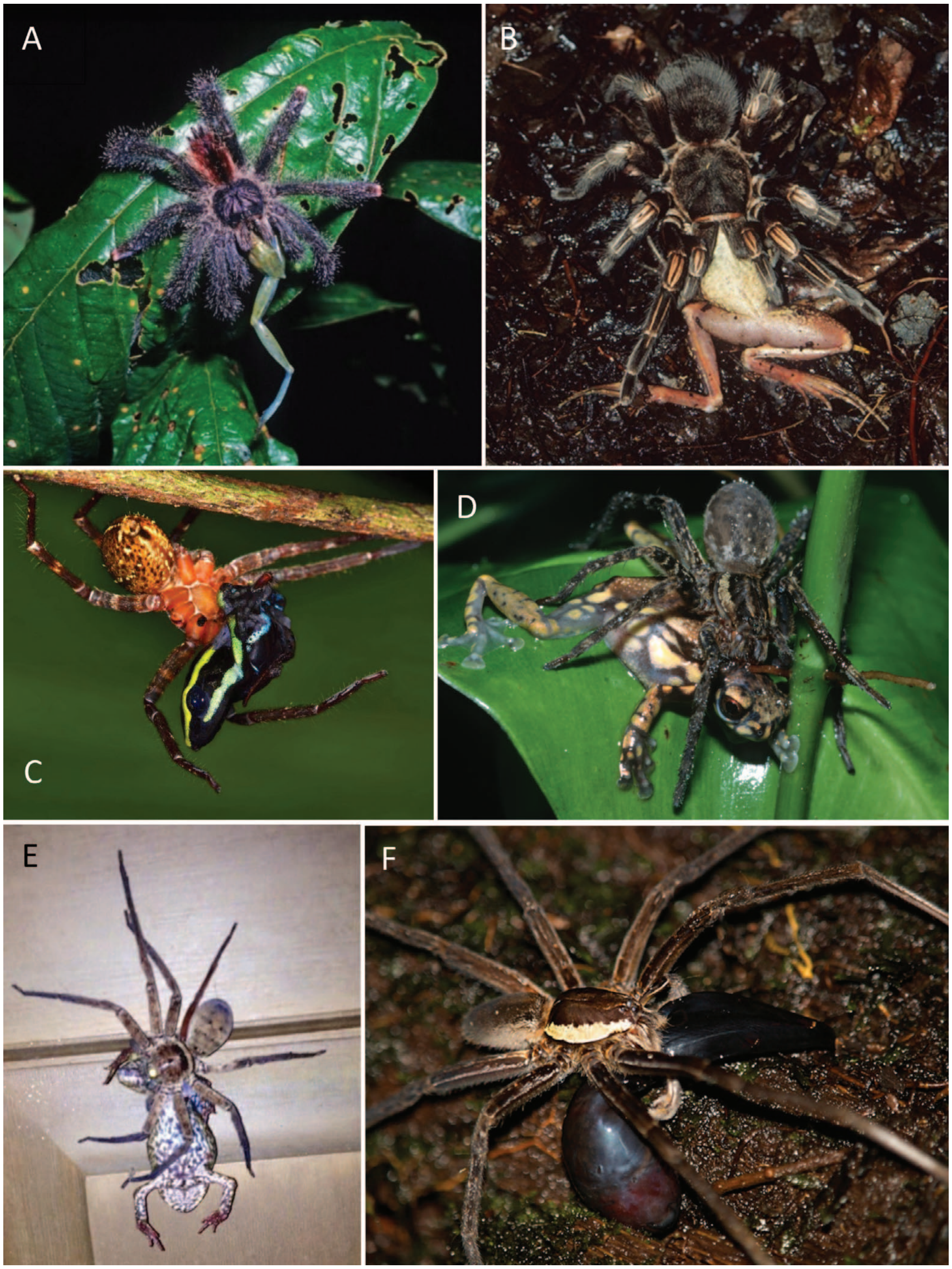

Figure 2.—**a** *Avicularia juruensis* (Theraphosidae) feeding on *Scarthyla goinorum* (Hylidae) in Peru (photo by Rick West, Sooke, British Columbia). **b** *Lasiodorides cf. striatus* (Theraphosidae) preying on unidentified frog in Peru (photo by Rick West). **c** *Ctenus medius* (Ctenidae) preying on poison-dart frog *Ameerega trivittata* (Dendrobatidae) in Surinam (photo by Trond Larsen, USA). **d** Ctenid spider (*Ancylometes* sp.) feeding on a male *Allophryne ruthveni* (Allophrynidae) in French Guiana (photo by Jean-Pierre Vacher, France). **e** *Heteropoda jugulans* (Sparassidae) eats cane toad *Rhinella marina* hanging on a door in Australia (photo by F. Pezzimenti). **f** Adult male of *Ancylometes* sp. (possibly *Ancylometes rufus*) feeding on frog tadpole (most likely Hylidae) near Samona Lodge, Cuyabeno Wildlife Reserve, Ecuador (photo by Ed Germain, Sydney, Australia).

in the temperate-cold regions. Second, the frequency of vertebrate predation by spiders is generally decreasing with increasing geographic latitude (see Nyffeler & Knörnschild 2013; Nyffeler & Pusey 2014; Nyffeler et al. 2017a,b) which has to do, among others, with the fact that larger spiders, such as ctenids, nephilids, or theraphosids, that are capable of overpowering vertebrate prey occur almost exclusively in warm, tropical or subtropical regions (e.g., Höfer & Brescovit 2000; Nyffeler & Knörnschild 2013; Borges et al. 2016; Carvalho et al. 2016). With regard to the temperate-cold regions, incidents of frog predation by fishing spiders (*Dolomedes* spp.) had been witnessed very rarely in or near

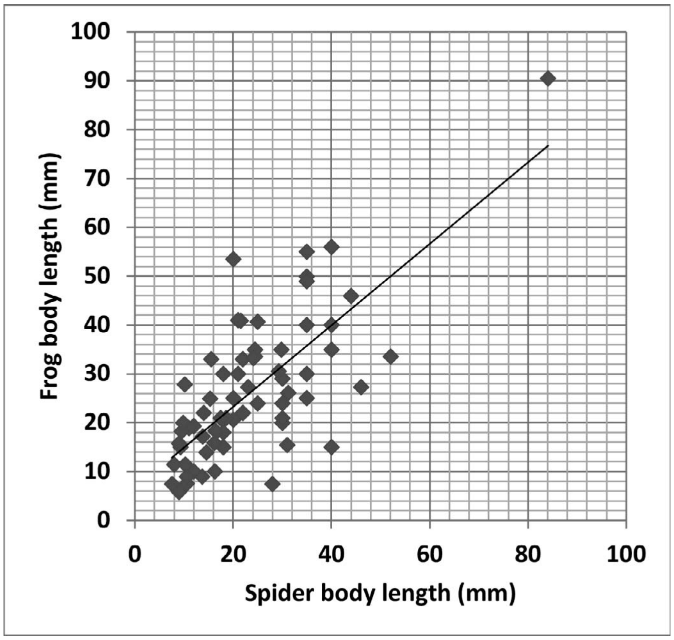

Figure 3.—Relationship between spider body length and frog body length (including post-metamorphs and tadpoles) based on 74 available data pairs. Frog body length refers to snout-vent length as regards post-metamorphs, whereas it refers to snout-vent length plus tail length as it regards tadpoles. Spider body length refers to cephalothorax plus abdomen. The frogs' body length was positively correlated with spider body length (r = 0.729).

ponds in Canada, Germany, Hungary, Romania, and the UK, while incidents of frog predation attributable to the orb-weaver *Argiope bruennichi* were reported from wetlands in Poland and Japan (see Supplementary material, online at http://dx.doi.org/10.1636/JoA-S-19-051.s1).

3.4 Predator-prey size ratio.—Spiders captured frogs which were between one-quarter and two times the spider's length. If spider body length is compared with tadpole total body length (snout-vent length + tail length), it follows that some spiders captured anuran prey that were up to 3 times their own length. This is in line with the results of a study from Florida in which the jumping spider *Phidippus regius* captured lizards of up to 3 times the spider's length (Nyffeler et al. 2017a). The capability of certain spiders to capture oversized frog prey has also been shown in a laboratory feeding trial; a captive fishing spider (*Nilus* sp.) of 0.435 g body mass was observed overpowering a frog 5.5 times heavier than the spider (Gudger 1925).

Spiders captured frogs that were both larger or smaller than their own body length (Fig. 3, also see Baba et al. 2019). The majority of frogs were somewhat larger than the spiders (mean subduing potential = 131% [± 6.5%] the spiders' body length; Fig. 3). The difference between average spider body length and average frog body length was statistically significant (Mann-Whitney U test, $n_1 = 96$, $n_2 = 118$, $Z = 2.831$, $P < 0.05$). Furthermore, frog body length was positively correlated with spider body length (r = 0.729; Fig. 3).

The fact that a large percentage of the reported spiders captured frogs that were larger than themselves is remarkable because spiders in general feed to a large extent on prey that are smaller than themselves (e.g., Nyffeler et al. 1992). The capability of certain spider groups (i.e., Ctenidae, Pisauridae, and Lycosidae) to overcome frogs of fairly large size relative to their own body size indicates that these spiders might be expert frog hunters that are evolutionarily well adapted to overpower this type of prey. The successful overpowering of oversized vertebrate prey by such spiders is facilitated by their use of potent neurotoxins (Nyffeler & Pusey 2014). In the case of large orb-weavers and black widows, the capability to subdue oversized vertebrate prey is additionally assisted by the use of strong catching webs and the ability to wrap prey (Figs. 1a,b; Nyffeler & Knörnschild 2013; Nyffeler & Vetter 2018).

4. DISCUSSION

4.1 Are the reported incidents real predation events?—It is arguable whether all incidents reported in this paper were real predation events or whether some were just cases of scavenging. Predation requires that a prey item must have been killed and eaten by the predator (Begon et al. 2005). Both behavioral traits, killing and consumption, have been witnessed multiple times by a large number of researchers in the wild and in captivity (e.g., Duellmann & Trueb 1994; Del-Grande & Moura 1997; Gopi Sundar 1998; Menin et al. 2005; Da Costa et al. 2006; Dehling 2007; Daza et al. 2008; Barbo et al. 2009; Bovo et al. 2014; Priyadarshana & Perera 2015). In the case of web-building spiders, evidence for predation is provided by the fact that these spiders immobilize frog victims by wrapping them in spider silk prior to administering one or several venomous bites (see Ganong & Folt 2015; Gilchrist 2017; Kirchmeyer et al. 2017). A dead frog wrapped in silk found hanging in a spider web was taken as proof that predation had occurred. A careful consideration of the 374 incidents reported in this paper led to the conclusion that the vast majority of these incidents referred to predation and not scavenging. Nevertheless, scavenging may occur on rare occasions if a hungry spider with an opportunistic feeding behavior encounters a frog carcass. For instance, there is an annecdotal report from the Neotropics that involved multiple theraphosids that were scavenging on the carcass of a road-killed bufonid, *Rhinella marina* (T. Mason, pers. comm.).

4.2 How important are frogs as spider diet?—The vast majority of spiders reported in this review (i.e., families Actinopodidae, Barychelidae, Ctenizidae, Dipluridae, Anyphaenidae, Clubionidae, Corinnidae, Dictynidae, Gnaphosidae, Lycosidae, Miturgidae, Nephilidae, Pisauridae, Salticidae, Theridiidae, and Trechaleidae) feed to a large extent on arthropod prey, and under most circumstances frogs are probably only marginal food for them. This is true in particular for spiders of high-latitude regions characterized by low to moderate temperatures (Zimmermann & Spence 1989; Szymkowiak et al. 2005). Exceptions include two mygalomorph species from Australia that are assumed to feed heavily on frogs. In Western Australia, Butler & Main (1959) found the remains of thirteen frogs in a single burrow of the trapdoor spider *Idiosoma rhaphiduca* (Idiopidae). In New South Wales, McKeown (1952) analyzed prey remains collected from webs of *Hadronyche formidabilis* (Atracidae) that were constructed on old pear trees. Besides dead beetles, the bones of countless tree frogs were detected in the webs, and after analyzing prey remains over a period of many months, McKeown concluded that tree frogs might be the chief diet of this spider in this particular region. Other reports on mygalomorph spiders as voracious frog-eaters originate from the Neotropics (Stewart 1985; Hillyard 2007; Ayroza et al. 2012; R. West, pers. comm.; Figs. 2a,b). In Puerto Rico, the arboreal theraphosid *Caribena laeta* was observed feeding heavily on coqui frogs (Stewart 1985). Many more quantitative investigations on the natural diets of tropical spiders are needed before reliable conclusions on the importance of frogs as spider food can be drawn.

4.3 Do spiders include poison arrow frogs in their diets?—A group of small-sized, brightly colored frogs with strong chemical defenses are termed 'dart-poison frogs' (family Dendrobatidae). These frogs, endemic to the tropical rainforests of Central and South America, are largely immune to predators due to highly toxic and bitter tasting alkaloids sequestered in their skin. A second family of toxic frogs termed as 'Malagasy poison frogs' (Mantellidae) occurs in Madagascar.

In Neotropical rainforests, a large variety of spider species occur sympatrically with dart-poison frogs (see Grant et al. 2006; Santos et al. 2017), and the question arises whether spiders actually are able to utilize such toxic frogs as prey or whether they are deterred by the frogs' skin toxins. Our literature survey provides evidence that spiders from at least five families (Ctenidae, Dipluridae, Nephilidae, Theraphosidae, and Trechaleidae) feed on poison frogs. This refers to the following spider species: *Ancylometes bogotensis*, *Cupiennius coccineus*, *Diplura* sp., *Nhandu cerradensis*, *Phoneutria nigriventer*, *Sericopelma rubronitens*, and *Trichonephila* sp.

Spiders have been observed feeding on the Brazil-nut poison frog *Adelphobates castaneoticus*, golden Mantella frog *Mantella aurantiaca*, green poison frog *Dendrobates auratus*, Lutz's poison frog *Ameerega flavopicta*, red-backed poison frog *Ranitomeya reticulata*, strawberry poison-dart frog *Oophaga pumilio*, and three-striped poison arrow frog *Ameerega triviatta* (Vollrath 1978; Caldwell & de Araujo 1998; Summers 1999; Da Costa et al. 2006; Gray et al. 2010; Acosta et al. 2013; Stynoski et al. 2014; Hantak et al. 2016; A. Gray, pers. comm.; T. Larsen, pers. comm.). An incident of a ctenid spider preying on a three-striped poison arrow frog *Ameerega triviatta* is depicted in Fig. 2c.

Not all encounters of spiders with dart-poison frogs resulted in the consumption of the frog. Folt & Lapinski (2017) observed an adult *Kiekie sinuatipes* attempting to capture an adult strawberry poison-dart frog. They wrote: "After the spider touched the frog with its front legs, it immediately rejected the frog which jumped away unharmed." Thus, there are cases in which dart-poison frogs were consumed by spiders and other cases in which they were rejected. Whether a poisonous frog is eaten or not may in a particular case depend on the spider's hunger level. So far, no incident of predation on the golden dart frog *Phyllobates terribilis* (a species considered to be the world's most toxic poison frog) by spiders has been reported.

If spiders were offered toxic frogs as prey under experimental conditions, a high percentage of these toxic prey were rejected, whereas equally-sized, nontoxic frogs were readily eaten by the same types of spiders (Szelistowski 1985; Gray et al. 2010; Stynoski et al. 2014; Murray et al. 2016). The fact that the bitter tasting dart-poison frogs are not the preferred prey is shown by the fact that spiders frequently wiped their chelicerae or pedipalps after biting a dart-poison frog (Summers 1999; Gray et al. 2010; Hantak et al. 2016). Spiders which consumed dart-poison frogs survived such incidents without apparent harm (Fig. 2c; Toft 1980; Summers 1999; Da Costa et al. 2006). Other than dendrobatid and mantellid frogs, other types of poisonous frogs are eaten by spiders. Spiders have been reported to occasionally kill and eat bufonids despite those bufadienolide-based defences (e.g., Raven 2000; Menin et al. 2005; Almeida et al. 2010; DeVore & Maerz 2014; Priyadarshana & Perera 2015).

4.4 How important are spiders as mortality agents of frogs?—Carnivorous vertebrates including reptiles, birds, and mammals are generally considered to be the major predators of frogs (Toledo et al. 2007). Especially snake predation is considered to be a very important source of frog mortality (Duellmann & Trueb 1994; Greene 2000; Toledo et al. 2007), but several studies suggest that spiders are among the most important invertebrate predators of frogs (Menin et al. 2005; Toledo 2005; Acosta et al. 2013). It has been hypothesized that snakes and spiders were the two most significant predator groups in terms of driving the evolution of defensive mechanisms in anurans (Jovanomic et al. 2009). However, since frog-catching spiders rely to a large extent on arthropods as a primary food source (e.g., T. Gasnier, pers. comm.; Lapinski & Tschapka 2013), they likely play a less important role as mortality agents of frogs compared to the anurophagous snakes. This is illustrated by a survey by Santos et al. (2016) in which snakes accounted for 69% of 36 documented frog predation incidents, whereas spiders accounted for 17% of 36 frog predation incidents. Frog-eating spiders occur in population densities many times higher than those of snakes and other carnivorous vertebrates (see Sierwald 1988; Moore & Townsend 1998; Vonesh 2003), and at least in tropical regions, spiders may have a considerable impact on the reproductive success and population dynamics of frogs (Villa et al. 1982; Hernández-Cuadrado & Bernal 2009; Rojas-Morales & Escobar-Lasso 2013). Predation by spiders on Neotropical frogs often occurs during the period of explosive breeding (e.g., Hernández-Cuadrado & Bernal 2009; J.-P. Vacher, pers. comm.). Further research will be needed before the impact of spider predation on frogs can be fully understood.

4.5 Spiders and frogs as competitors and intraguild predators.—Spiders and frogs are competitors and intraguild predators (*sensu* Polis et al. 1989) that prey to a large extent on arthropods. Especially in tropical forested areas these two predator groups can exert considerable predation pressure on the arthropod fauna (see Nyffeler & Birkhofer 2017; Nyffeler et al. 2018). Occasionally these two predator groups are eating each other ("cross-predation"; e.g., Gaiarsa et al. 2012). Whether a frog is the hunter or the hunted depends on the spider/frog size ratio and the opponents' hunting strategies and defenses. While some spiders frequently overpower frogs that are larger than themselves, frogs exclusively kill spiders of smaller size than themselves (Labanick 1976; Parmelee 1999; Hirai & Matsui 2002; Arroyo et al. 2008). This behavioral difference can be explained by the fact that spiders have an extra-intestinal digestion (i.e., they digest prey outside their body), whereas frogs must swallow prey in order to digest it. Frogs from many different families feed on a variety of spider taxa (Lamb 1984; Santos et al. 2004; Çiçek & Mermer 2007; Fonseca-Pérez et al. 2017). Especially tropical rain forest tree frogs (Hylidae) may include a high proportion of spiders in their diets (Van Sluys & Rocha 1998; Menéndez-Guerrero 2001; Vaz-Silva et al. 2003; Solé & Pelz 2007). Spiders devoured by frogs are usually only a few millimeters in length, but there are exceptional cases in which frogs eat large spiders (see Toft 1980; Teixeira & Coutinho 2002; Teixeira & Vrcibradic 2003). For example, giant pacman frogs (Ceratophryidae) are so large and powerful that they can kill and swallow even theraphosid spiders of ≈4 cm body length (Anonymous 2011).

5. CONCLUDING REMARKS

In previous global surveys, frog predation was documented for ≤10 spider families (Menin et al. 2005; Toledo 2005; Babangenge et al. 2019). We were able to document that spiders from 22 families (= 18.3% of the 120 recognized families, see World Spider Catalog 2019) eat frogs. And while according to previous reviews, frogs from only 7–10 families were reported to be victims of spider predation (Menin et al. 2005; Toledo 2005; Babangenge et al. 2019), we were able to show that the list of frog victims is much longer encompassing a total of 32 families. Wherever frogs occur, they share their habitats with spiders resulting in predator-prey encounters between these two predator groups. Many of these predation events occur during the night hours in remote tropical forests and swamplands, which makes their observation very difficult (Nyffeler & Pusey 2014). One can speculate that a high percentage of the ≈7,100 described frog species (see Frost 2019) are vulnerable to spider predation at some point in their life cycle during which time they reach a body size to be catchable by certain spiders. Some frog species, however, are avoided as prey (see Cocroft & Hambler 1989). Our finding that such a high diversity of spider taxa is utilizing such a high variety of frog taxa as prey is novel.

The global spider community, that weighs an estimated 25 million tons, is assumed to consume about 400–800 million tons of prey per year (Nyffeler & Birkhofer 2017). To satisfy these enormous energy requirements spiders must acquire enough food from a broad variety of food sources (i.e., large diet breadth) that includes different types of invertebrates, small vertebrates, and even plant matter (also see Nyffeler & Symondson 2001; Nyffeler & Knörnschild 2013; Nyffeler & Pusey 2014; Nyffeler et al. 2016, 2017a,b; Nyffeler & Vetter 2018). The utilization of >200 frog species as supplementary prey is enhancing the food supply of the global spider community, and this is presumed to increase the spiders' survival capability, which might be of particular ecological importance in tropical forested areas known for high abundance and species richness of frogs and spiders.

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APPENDIX 1

List of frog-eating spider species. * indicates observed exclusively under laboratory conditions

CURSORIAL HUNTERS

Anyphaenidae
1. *Patrera armata* (Chickering, 1940)

Clubionidae
2. *Clubiona* sp.

Corinnidae
3. Unidentified sp.

Ctenidae
4. *Ancylometes bogotensis* (Keyserling, 1877); 5. *Ancylometes concolor* (Perty, 1833); 6. *Ancylometes hewitsoni* (F.O. Pickard-Cambridge, 1897); 7. *Ancylometes rufus* (Walckenaer, 1837); 8. *Ctenus amphora* Mello-Leitão, 1930; 9. *Ctenus medius* Keyserling, 1891; 10. *Ctenus ornatus* (Keyserling, 1877); 11. *Ctenus ottleyi* (Petrunkevitch, 1930); 12. *Ctenus rectipes* F.O. Pickard-Cambrige, 1897; 13. *Ctenus villasboasi* Mello-Leitão, 1949; 14. *Kiekie curvipes* (Keyserling, 1881); 15. *Kiekie sinuatipes* (F.O. Pickard-Cambridge, 1897); 16. *Ohvida vernalis* (Bryant, 1940); 17. *Phoneutria* cf. *bahiensis*; 18. *Phoneutria boliviensis* (F.O. Pickard-Cambrige, 1897); 19. *Phoneutria fera* Perty, 1833; 20. *Phoneutria nigriventer* (Keyserling, 1891); 21. *Piloctenus* cf. *haematostoma*

Dictynidae
22. *Argyroneta aquatica* (Clerck, 1757)*

Gnaphosidae
23. Unidentified sp.

Lycosidae
24. *Aglaoctenus oblongus* (C.L. Koch, 1847); 25. *Allocosa obscuroides* (Strand, 1906); 26. *Arctosa* sp.; 27. *Diapontia uruguayensis* Keyserling, 1877; 28. *Hogna carolinensis* (Walckenaer, 1805); 29. *Hogna* sp. [a different species than *H. carolinensis* since this latter species does not occur in Brazil]; 30. *Lycosa carmichaeli* Gravely, 1924; 31. *Lycosa erythrognatha* Lucas, 1836; 32. *Lycosa pampeana* Holmberg, 1876; 33. *Lycosa* cf. *thorelli*; 34. *Pardosa pseudoannulata* (Bõsenberg & Strand, 1906)*; 35. *Pirata piraticus* (Clerck, 1757)*; 36. *Pirata piscatorius* (Clerck, 1757)*; 37. *Tasmanicosa godeffroyi* (L. Koch, 1865)?; 38. *Tigrosa helluo* (Walckenaer, 1837); 39. *Venatrix lapidosa* (McKay, 1974); 40. *Wadicosa fidelis* (O. Pickard-Cambridge, 1872)

Miturgidae
41. *Miturga* sp.

Pisauridae
42. *Dolomedes albineus* Hentz, 1845; 43. *Dolomedes facetus* L. Koch, 1876; 44. *Dolomedes fimbriatus* (Clerck, 1757); 45. *Dolomedes holti* Carico, 1973; 46. *Dolomedes okefinokensis* Bishop, 1924; 47. *Dolomedes orion* Tanikawa, 2003; 48. *Dolomedes plantarius* (Clerck, 1757); 49. *Dolomedes raptor* Bõsenberg & Strand 1906; 50. *Dolomedes scriptus* Hentz, 1845; 51. *Dolomedes sulfureus* L. Koch, 1878; 52. *Dolomedes tenebrosus* Hentz, 1844 ?; 53. *Dolomedes triton* (Walckenaer, 1837); 54. *Dolomedes vittatus* Walckenaer, 1837; 55. *Megadolomedes australianus* (L. Koch, 1865); 56. *Nilus* cf. *albocinctus*; 57. *Nilus curtus* O. Pickard-Cambrige, 1876; 58. *Nilus margaritatus* (Pocock, 1898) 59. *Nilus radiatolineatus (*Strand, 1906); 60. *Nilus rubromaculatus* (Thorell, 1899)?; 61. *Thaumasia velox* Simon, 1898

Salticidae
62. *Hasarius* sp. ? [a genus other than *Phidippus*]; 63. *Phidippus regius* C.L. Koch, 1846

Sparassidae
64. *Heteropoda jugulans* (L. Koch, 1876); 65. *Heteropoda natans* Jäger, 2005*; 66. *Heteropoda* cf. *simplex*; 67. *Neosparassus* sp.; 68. *Olios* sp.

Theraphosidae
69. *Aphonopelma hentzi* (Girard, 1852)*; 70. *Avicularia avicularia* Linnaeus, 1758; 71. *Avicularia juruensis* Mello-Leitão, 1923; 72. *Brachypelma smithi* (F.O. Pickard-Cambridge, 1897); 73. *Caribena laeta* (C.L. Koch, 1842; 74. *Cyriopagopus schmidti* (von Wirth, 1991)*; 75. *Lasiodora curtior* Chamberlin, 1917*; 76. *Lasiodorides* cf. *striatus*; 77. *Nhandu cerradensis* Bertani, 2001; 78. *Orphnaecus kwebaburdeos* (Barrion-Dupo, Barrion & Rasalan, 2015)*; 79. *Pamphobeteus* sp.; 80. *Selenocosmia crassipes* (L. Koch, 1874)*; 81. *Selenocosmia stirlingi* Hogg, 1901; 82. *Selenotypus* sp.; 83. *Sericopelma rubronitens* Ausserer, 1875; 84. *Theraphosa blondi* (Latreille, 1804); 85. *Vitalius* sp. [possibly *Vitalius roseus* (Mello-Leitão, 1923)]; 86. *Xenesthis immanis* (Ausserer, 1875)

Trechaleidae
87. *Cupiennius coccineus* F.O. Pickard-Cambridge, 1901; 88. *Cupiennius getazi* Simon, 1891; 89. *Cupiennius salei* (Keyserling, 1877); 90. *Neoctenus* sp.; 91. *Trechalea* sp.; 92. *Trechaleoides biocellata* (Mello-Leitão, 1926); 93. *Trechaleoides keyserlingi* (F.O. Pickard-Cambridge, 1903)

AERIAL-WEB WEAVERS

Araneidae
94. *Acanthepeira stellata* (Walckenaer, 1805); 95. *Argiope aurantia* Lucas, 1833; 96. *Argiope bruennichi* (Scopoli 1772); 97. *Cyrthophora citricola* (Forsskål, 1775); 98. *Eriophora edax* (Blackwall, 1863); 99. *Eriophora fuliginea* (C.L. Koch, 1838); 100. *Parawixia kochi* (Taczanowski, 1873); 101. *Parawixia* sp. (different species than #100, because *Parawixia kochi* does not occur in Singapore)

Nephilidae
102. *Trichonephila clavipes* (Linnaeus, 1767); 103. "*Tricho-*

nephila" sp. ? [a species different from #102, because *T. clavipes* does not occur in Madagascar]

Theridiidae
104. *Latrodectus geometricus* C.L. Koch, 1841; 105. *Latrodectus hesperus* Chamberlin & Ivie, 1935

FUNNEL-WEB WEAVERS

Atracidae
106. *Atrax robustus* O. Pickard-Cambridge, 1877; 107. *Hadronyche formidabilis* (Rainbow, 1914); 108. *Hadronyche valida* (Rainbow & Pulleine, 1918)

Dipluridae
109. *Diplura* sp.; 110. *Linothele megatheloides* Paz & Raven, 1990

TRAPDOOR-BUILDERS

Actinopodidae
111. *Missulena bradleyi* Rainbow, 1914; 112. *Missulena occatoria* Walckenaer, 1805

Barychelidae
113. Unidentified sp.

Ctenizidae
114. *Cteniza* sp.

Idiopidae
115. *Gaius villosus* Rainbow, 1914; 116. *Idiosoma rhaphiduca* (Rainbow & Pulleine, 1918)

APPENDIX 2

List of frog species reported as victims of spider predation. – *Feeding on frogs observed in captivity. Life stage of anuran prey indicated in parenthesis behind scientific name: E = Egg/embryo, H = Hatchling, T = Tadpole, M = Metamorph, P = Post-metamorph

Allophrynidae
1. *Allophryne ruthveni* (P)

Aromobatidae
2. *Allobates brunneus* (P); 3. *Allobates insperatus* (P); 4. *Anomaloglossus stepheni* (P); 5. *Mannophryne collaris* (P); 6. *Rheobates palmatus* (P)

Arthroleptidae
7. *Leptopelis brevirostris* (P)

Brachycephalidae
8. *Ischnocnema cf. parvua* (P)

Bufonidae
9. *Adenomus kelaarthii* (P); 10. *Amazophrynella minuta* (P); 11. *Anaxyrus americanus* (P); 12. *Anaxyrus terrestris* (P); 13. *Barbarophryne brongersmai* (P); 14. *Bufo bufo** (T); 15. *Duttaphrynus stomaticus* (P); 16. *Rhaebo haematiticus* (P); 17. *Rhinella granulosa* (P); 18. *Rhinella humboldti* (P); 19. *Rhinella marina* (H, M, P); 20. *Rhinella ornata* (M); 21. *Rhinella spinulosa** (T); 22. *Schismaderma carens** (T); 23. *Sclerophrys regularis** (P)

Centrolenidae
24. *Centrolene quindianum* (E); 25. *Cochranella mache* (P); 26. *Espadarana prosoblepon* (P); 27. *Hyalinobatrachium colymbiphyllum* (E); 28. *Hyalinobatrachium fleischmanni* (P); 29. *Rulyrana orejuela* (P); 30. *Teratohyla spinosa* (E, P)

Ceratobatrachidae*
31. *Platymantis dorsalis** (P)

Craugastoridae
32. *Barycholos ternetzi* (P); 33. *Craugastor alfredi* (P); 34. *Craugastor bransfordii* (P); 35. *Craugastor fitzingeri* (P); 36. *Craugastor pygmaeus* (P); 37. *Craugastor ranoides* (P); 38. *Craugastor stejnegerianus* (P); 39. *Pristimantis cerasinus* (P); 40. *Pristimantis gaigeae* (N/A); 41. *Pristimantis medemi* (P); 42. *Pristimantis peruvianus* (P); 43. *Pristimantis ramagii* (P); 44. *Pristimantis ridens* (P)

Cycloramphidae
45. *Cycloramphus boraceiensis* (P); 46. *Thoropa miliaris* (N/A)

Dendrobatidae
47. *Adelphobates castaneoticus* (T, P); 48. *Ameerega flavopicta* (P); 49. *Ameerega trivittata* (P); 50. *Dendrobates auratus* (P); 51. *Oophaga pumilio* (P); 52. *Ranitomeya reticulata* (T)

Dicroglossidae
53. *Euphylyctis cyanophlyctis* (P)

Eleutherodactylidae
54. *Eleutherodactylus coqui* (P); 55. *Eleutherodactylus cuneatus* (P); 56. *Eleuterodactylus zugi* (N/A)

Hemiphractidae
57. *Hemiphractus scutatus* (P)

Hylidae
58. *Acris blanchardi* (P); 59. *Acris crepitans* (P); 60. *Acris gryllus* (M, P); 61. *Aplastodiscus albosignatus* (P); 62. *Aplastodiscus arildae* (P); 63. *Boana albopunctata* (P); 64. *Boana bischoffi* (P); 65. *Boana crepitans* (E); 66. *Boana fasciata* (P); 67. *Boana geographica* (P); 68. *Boana multifasciata* (P); 69. *Boana pulchella* (P); 70. *Dendrosophus bifurcus* (P); 71. *Dendropsophus branneri* (P); 72. *Dendropsophus brevifrons* (P); 73. *Dendropsophus ebraccatus* (P); 74. *Dendropsophus elegans* (P); 75. *Dendropsophus haddadi* (P); 76. *Dendropsophus kamagarini* (P); 77. *Dendropsophus leali* (P); 78. *Dendropsophus leucophyllatus* (P); 79. *Dendropsophus melanargyreus* (P); 80. *Dendropsophus microcephalus* (P); 81. *Dendropsophus microps* (P); 82. *Dendropsophus minutus* (M, P); 83. *Dendropsophus nanus* (M); 84. *Dendropsophus pseudomeridianus* (T); 85. *Dendropsophus sanborni* (P); 86. *Dendropsophus sarayacuensis* (P); 87. *Dendrosophus werneri* (P); 88. *Dryophytes cinereus* (P); 89. *Dryophytes femoralis* (M, P); 90. *Dryophytes japonicus* (N/A); 91. *Dryophytes squirellus* (P); 92. *Dryophytes versicolor* (M); 93. *Duellmanohyla rufioculis* (P); 94. *Hyliola regilla* (P); 95. *Hyloscirtus palmeri* (P); 96. *Itapotihyla langsdorffii* (T); 97. *Lysapsus limellum* (P); 98. *Ololygon alcatraz* (P); 99. *Ololygon aromothyella* (T); 100. *Ololygon littoralis* (P); 101. *Osteocephalus taurinus* (P); 102. *Osteopilus septentrionalis* (P); 103. *Phyllodytes luteolus* (P); 104. *Pseudacris crucifer* (P); 105. *Pseudacris feriarum* (P); 106. *Pseudacris ocularis* (P); 107.

Rheohyla miotympanum (P); 108. *Scarthyla goinorum* (P); 109. *Scinax alter* (P); 110. *Scinax crospedospilus* (P); 111. *Scinax cruentomma* (P); 112. *Scinax elaeochroa* (P); 113. *Scinax fuscomarginatus* (N/A); 114. *Scinax fuscovarius* (P); 115. *Scinax garbei* (P); 116. *Scinax ictericus* (P); 117. *Scinax similis* (P); 118. *Scinax squalirostris* (P); 119. *Scinax ruber* (P); 120. *Smilisca sordida* (P); 121. *Sphaenorhynchus lacteus* (N/A); 122. *Tlalocohyla loquax* (P); 123. *Tripion spinosus* (P); 124. *Trachycephalus typhonius* (T)

Hylodidae
125. *Crossodactylus schmidti* (P); 126. *Hylodes phyllodes* (P)

Hyperoliidae
127. *Afrixalus vibekensis* (P); 128. *Heterixalus tricolor* (P); 129. *Hyperolius argus* (P); 130. *Hyperolius baumanni* (P); 131. *Hyperolius fusciventris* (P); 132. *Hyperolius glandicolor* (N/A); 133. *Hyperolius marmoratus* (P); 134. *Hyperolius microps* (N/A); 135. *Hyperolius nitidulus* (P); 136. *Hyperolius phantasticus* (P); 137. *Hyperolius pusillus* (P); 138. *Hyperolius spinigularis* (M, P); 139. *Hyperolius sylvaticus* (P)

Leptodactylidae
140. *Adenomera andreae* (P); 141. *Adenomera hylaedactyla* (P); 142. *Adenomera marmorata* (P); 143. *Engystomops petersi* (P); 144. *Engystomops pustulosus* (E, P); 145. *Leptodactylus didymus* (P); 146. *Leptodactylus fragilis* (N/A); 147. *Leptodactylus fuscus* (P); 148. *Leptodactylus insularum* (T); 149. *Leptodactylus knudseni* (P);150. *Leptodactylus latinasus* (E); 151. *Leptodactylus latrans* (T); 152. *Leptodactylus wagneri** (P); 153. *Physalaemus albonotatus* (P); 154. *Physalaemus camacan* (P); 155. *Physalaemus cuvieri* (P); 156. *Physalaemus olfersii* (P); 157. *Physalaemus spiniger* (N/A); 158. *Pleurodema bufonium* (T); 159. *Pseudopaludicola mystacalis* (P); 160. *Pseudopaludicola pocoto* (P)

Limnodynastidae
161. *Adelotus brevis* (P); 162. *Neobatrachus sudelli* (P)

Mantellidae
163. *Mantella aurantiaca* (P)

Megophryidae*
164. *Leptobrachium montanum** (T)

Microhylidae
165. *Chiasmocleis* sp. (P); 166. *Elachistocleis panamensis* (P); 167. *Hamptophryne boliviana* (P); 168. *Microhyla butleri* (P); 169. *Microhyla ornata* (P)

Myobatrachidae
170. *Crinia pseudinsignifera* (P); 171. *Crinia signifera* (P)

Pelodryadidae
172. *Litoria fallax* (P); 173. *Litoria olongburensis* (P); 174. *Litoria rubella* (P); 175. *Litoria tornieri* (P); 176. *Ranoidea caerulea* (P); 177. *Ranoidea dayi* (P); 178. *Ranoidea gracilenta* (P); 179. *Ranoidea lesueurii* (P); # N/A. *Ranoidea* sp. (M)

Phrynobatrachidae
180. *Phrynobatrachus natalensis** (P)

Phyllomedusidae
181. *Agalychnis callidryas* (E, T, P); 182. *Phyllomedusa vaillantii* (N/A); 183. *Pithecopus nordestinus* (T); 184. *Pithecopus palliatus** (P)

Pipidae
185. *Pipa arrabali* (P); 186. *Xenopus laevis** (T, P); 187. *Xenopus mellotropicalis* (T)

Pyxicephalidae
188. *Pyxicephalus adspersus* (M); 189. *Strongylopus fasciatus** (P); 190. *Tomopterna cryptotis* (T)

Ranidae
191. *Amnirana albolabris* (T); 192. *Chalcorana raniceps* (M); 193. *Lithobates catesbeianus* (T); 194. *Lithobates clamitans* (M, P); 195. *Lithobates sylvaticus* (T); 196. *Lithobates warszewitschii* (P); 197. *Odorrana narina* (P); 198. *Pulchrana picturata* (P); 199. *Rana temporaria* (T, P); 200. *Rana ulma* (P)

Ranixalidae
201. *Indirana* sp. (T)

Rhacophoridae
202. *Chiromantis doriae* (P); 203. *Chiromantis nongkhorensis* (P); 204. *Feihyla hansenae* (E); 205. *Philautus vermiculatus* (P); 206. *Philautus* sp. (a different species than #205; *P. vermiculatus* not found in India) (P); 207. *Zhangixalus viridis* (M)

Scaphiopodidae
208. *Spea multiplicata* (P)

Telmatobiidae
209. *Telmatobius oxyxcephalus* (P)