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REVIEW

Spiders feeding on vertebrates is more common and widespread than previously thought, geographically and taxonomically

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Abstract. According to a recent global literature survey, a total of 39 out of the 129 known spider families (~30%) contain species capable of capturing vertebrate prey. The finding that the percentage of spider families engaged in vertebrate predation is so high is novel. Two groups of vertebrate-eating spiders are distinguished: "habitual vertebrate-eaters" vs. "occasional vertebrate-eaters". The habitual vertebrate-eaters comprise ten spider families (Araneidae, Atracidae, Ctenidae, Lycosidae, Nephilidae, Pisauridae, Theraphosidae, Theridiidae, Trechaleidae, and Sparassidae) to which can be attributed 91% of all reported vertebrate predation incidents. The habitual vertebrate-eaters have evolved prey-capture adaptations such as (1) sufficient physical strength coupled with large body size, (2) the use of potent venoms, and (3) the use of highly efficient prey-catching webs. By contrast, unexpected feeding on vertebrates by the occasional vertebrate-eaters (i.e., Actinopodidae, Agelenidae, Amaurobiidae, Anyphaenidae, Barychelidae, Clubionidae, Corinnidae, Ctenizidae, Cyrtaucheniidae, Deinopidae, Desidae, Dipluridae, Eresidae, Filistatidae, Gnaphosidae, Haplonoproctidae, Linyphiidae, Liocranidae, Miturgidae, Oxyopidae, Pholcidae, Porrhothelidae, Salticidae, Selenopidae, Sicariidae, Sparassidae, Tetragnathidae, and Thomisidae) might be considered as chance events that took place when a tiny vertebrate crossed the path of an opportunistic spider. For a few families (e.g., Idiopidae) their status as habitual or occasional vertebrate predators is still unclear. In conclusion, our survey unveiled a large number of spider taxa previously not anticipated to feed on vertebrate prey. These findings improve our general understanding of spider feeding ecology and provide a first assessment of the significance of vertebrate prey as a food source for spiders.

Keywords: Araneae, predator diversity, vertebrate prey, prey-capture adaptations, physical strength, toxins, silk tensile strength

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1. INTRODUCTION

In biology text books of the past, the narrative was upheld that spiders would feed more or less exclusively on arthropods (Bristowe 1941; Gertsch 1979; Foelix 1982). Anecdotal observations of predation on unusual prey such as fish, frogs, lizards or birds were considered to represent either extremely rare chance events or doubtful reports. So for instance, Foelix (1982) stated in the first edition of his book *Biology of Spiders* "....It is rather unusual to find vertebrates among a spider's prey, although tadpoles or small fish may fall victim to certain lycosids or pisaurids. Reports that claim that large 'tarantulas' have been feeding on birds, lizards, or snakes are rarely scientifically verifiable." However, during the last 40 years much photographic evidence of vertebrate predation by spiders has been reported in the scientific literature and in the social media, providing irrefutable proof that this type of

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feeding behavior is not that uncommon in at least some spider groups (e.g., McCormick & Polis 1982; Menin et al. 2005; Toledo 2005; Nyffeler & Knörnschild 2013; Nyffeler & Pusey 2014; Folt & Lapinski 2017; Nyffeler & Vetter 2018; Babangenge et al. 2019; Nyffeler & Altig 2020; Reyes-Olivares et al. 2020; Nyffeler & Gibbons 2021). In the following, we provide an overview of geographically and taxonomically widespread vertebrate predation by different spider families.

2. METHODS

2.1 Data collection.—A global survey of scientific literature and social media reports, using the search method described in Nyffeler et al. (2017a), resulted in a total of 966 recorded incidents (source: McCormick & Polis 1982; Brooks 2012; Nyffeler & Knörnschild 2013; Nyffeler & Pusey 2014; Nyffeler et al. 2017a, 2021; Nyffeler & Vetter 2018; Weisberger 2019; Nyffeler & Altig 2020; Reyes-Olivares et al. 2020; Fulgence et al. 2021; Nyffeler & Gibbons 2021, 2022; Google Scholar & Google Picture Survey for Sparassidae feeding on vertebrates 2021). From this database, we extracted the following:

– How many times each spider family had been engaged in vertebrate predation. By comparing the frequency with which the 39 spider families were engaged in vertebrate predation, it was possible to distinguish two groups: "habitual vertebrate-eaters" vs. "occasional vertebrate-eaters."

– For each spider family how many of nine major geographic regions (Europe, Africa, Asia, Australia, North America, Central America, South America, the Caribbeans, and Antarctica) vertebrate predation had been reported in the scientific literature and social media. We ranked these to get an approximate measure of the geographical extent of this type of feeding behavior for each family of spiders.

– For each spider family, how many of five different vertebrate categories (i.e., amphibians, reptiles, fish, birds, and mammals; Table 1) were part of the diet. This information provides a rough measure for dietary diversity of a particular spider family.

2.2 Statistical methods.—The two-tailed Mann-Whitney *U* test (see MacFarland & Yates 2016) was applied to examine whether mean values differed statistically significantly. These analyses were performed online at https://www.socscistatistics.com/tests/mannwhitney/default2.aspx. Prior to that, we examined with the Shapiro-Wilk test software whether the data were normally distributed (Online at http://www.statskingdom.com/320ShapiroWilk.html). As the data gathered in our survey were not normally distributed, we used a nonparametric Mann-Whitney *U* test. Mean values are followed by Standard Errors (± SE).

2.3 Taxonomic comments.—Nomenclature of spider taxa was based on the World Spider Catalog 2022 except for the nephilids. Contrary to the World Spider Catalog 2022, we placed the genera *Nephila* Leach, 1815, *Nephilingis* Kuntner, 2013, and *Trichonephila* Dahl, 1911 in the family Nephilidae (*sensu* Kuntner et al. 2019). *Argyroneta aquatica* (Clerck, 1757) previously placed in the family Cybaeidae has been transferred to Dictynidae (World Spider Catalog 2022).

Spiders depicted in photos (Figs. 2, 4–6) were identified by the following spider taxonomists: Agelenidae (P. Jäger, G. Oxford), Anyphaenidae (A. Brescovit), Araneidae (G.B. Edwards), Ctenidae (A. Brescovit, H. Höfer), Deinopidae (A. Austin, R. Raven), Nephilidae (M. Kuntner, I-Min Tso), Pholcidae (G. Ackermann, B. Huber), Pisauridae (R. Raven), Theridiidae (L.L.C. Jones), and Thomisidae (A. Dippenaar-Schoeman).

Vertebrates depicted in photos (Figs. 2, 4–6) were identified by the following vertebrate taxonomists: Anura (A. Amey), Aves (D.S. Frank), Chiroptera (K. Armstrong, M. Craig, D. Milne, C. Pavey, T. Reardon, M. Rhodes, C. Tidemann), Pisces (R. Vari), Serpentes (J.W. Gibbons, L.L.C. Jones), Squamata / Gekkonidae (G. Alexander, A. Bauer, W. Conradi), Squamata / Lacertidae (V. Albouy, F. Braña, P-A. Crochet, I. Ineich), and Squamata / Scincidae (R. Shine).

3. RESULTS

3.1 General information on vertebrate-eating spiders.—Vertebrate predation by spiders is a global phenomenon found on all continents except Antarctica (Nyffeler & Knörnschild 2013; Nyffeler & Pusey 2014; Nyffeler & Altig 2020; Nyffeler & Gibbons 2021). Geographic areas from which vertebrate predation has been most frequently reported are the Neotropics, North America, and Australia. These regions combined constituted ~70% of all recorded cases. Reports of vertebrate predation were less common in Africa, Asia, and Europe (combined ~30% of the recorded cases). Although predation on vertebrates is found predominantly in the warmer regions of the globe (see Nyffeler & Knörnschild 2013; Nyffeler & Pusey 2014; Nyffeler & Altig 2020; Nyffeler & Gibbons 2021), numerous accounts of vertebrate-eating by spiders have been reported from habitats located in the temperate climate zone (e.g., B. Thaler-Knoflach, pers. comm.; R. Jacob, pers. comm.; Zimmermann & Spence 1989; Szymkowiak et al. 2005; Nyffeler & Pusey 2014; Dunbar et al. 2018; Nyffeler & Altig 2020; Nyffeler & Gibbons 2021).

In the current study, the overall mean body length of spiders preying on vertebrates was 20.35 ± 1.83 mm (median = 17.50 mm, $n = 39$ spider families; Table 1). Spiders have been documented to feed on an impressively wide variety of different vertebrate groups including birds (Aves), bats (Chiroptera), mice (Muridae), deer mice (Cricetidae), voles (Cricetidae), shrews (Soricidae), rats (Muridae), mouse lemurs (Cheirogaleidae), mouse opossums (Didelphidae), pygmy possums (Burramyidae), fish (Osteichthyes), frogs (Anura), toads (Anura), snakes (Serpentes), lizards (Squamata), newts (Salamandridae), lungless salamanders (Plethodontidae), mole salamanders (Ambystomatida), and caecilians (Caeciliidae) (e.g., Raven 1990; Menin et al. 2005; Toledo 2005; Pastorelli & Laghi 2007; Brooks 2012; Nyffeler & Knörnschild 2013; Nyffeler & Pusey 2014; Nyffeler & Vetter 2018; Koumoundouro 2019; von May et al. 2019; Nyffeler & Altig 2020; Nyffeler & Gibbons 2021). Amphibians and reptiles constituted the most frequently documented vertebrate prey of spiders (~2/3 of all documented cases; Table 1; Figs. 2C, E, 4–6).

3.2 Diversity of spider families engaged in vertebrate predation.—In past reviews only roughly a dozen spider families were reported to be engaged in vertebrate predation (McCormick & Polis 1982; Menin et al. 2005; Toledo 2005; Folt & Lapinski 2017; Babangenge et al. 2019; Reyes-Olivares et al. 2020). In the present paper, we show that a total of 39 out of the 129 known spider families (~30%) contain at least

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Table 1.—Spider families containing species engaged in vertebrate predation and corresponding prey types. Symbols: • = evidence of predation. (•) = mouse killed in a *Tegenaria* funnel web, but no evidence of eating the dead mouse. [•] = Marsupial mouse trapped in trapdoor spider's burrow; unsure if it was later eaten by the spider. ○ = fish and tadpoles killed and eaten in aquarium. Δ = tiny live fish put into an *Argiope* web was killed and eaten. (□) = dead fish, offered in captivity, were consumed. Foraging strategies: WEB = web-based hunters; BT = burrow with trapdoor; HUNT = hunters without webs.

#	Spider family	Foraging strategy	Spider body length in mm; Range (Mean)	Prey type				
				Amphibians	Reptiles	Fish	Birds	Mammals
01	Actinopodidae	BT	10–35 (22.5)	•	•			
02	Agelenidae	WEB	13.5–18 (15.75)	•	•			(•)
03	Amaurobiidae	WEB	8.5 (8.5)	•				
04	Anyphaenidae	HUNT	8.5 (8.5)	•				
05	Araneidae	WEB	13–30 (21.5)	•	•	Δ	•	•
06	Atracidae	WEB	10–50 (30)	•	•		•	○
07	Barychelidae	BT	30 (30)	•	•			
08	Clubionidae	HUNT	14.5 (14.5)	•				
09	Corinnidae	HUNT	8–14.5 (11.25)	•				
10	Ctenidae	HUNT	8–46 (27)	•	•	•	•	•
11	Ctenizidae	BT	28 (28)	•				
12	Cyrtaucheniidae	BT	15 (15)				•	
13	Deinopidae	WEB	20 (20)		•			
14	Desidae	HUNT	10–15 (12.5)			○		
15	Dictynidae	WEB	15 (15)	○		○		
16	Dipluridae	WEB	28 (28)	•	•			
17	Eresidae	WEB	10–20 (15)		•			
18	Filistatidae	WEB	14 (14)		•			
19	Gnaphosidae	HUNT	10–15 (12.5)	•				
20	Halonoproctidae	BT	28 (28)		•			
21	Idiopidae	BT	20–35 (27.5)	•	•		•	[•]
22	Linyphiidae	WEB	7 (7)		•			
23	Liocranidae	HUNT	7 (7)			•		
24	Lycosidae	HUNT	6.5–40 (23.25)	•	•	•		•
25	Miturgidae	HUNT	15–20 (17.5)	•				
26	Nephilidae	WEB	10–70 (40)	•	•		•	•
27	Oxyopidae	HUNT	15 (15)		•			
28	Pholcidae	WEB	10 (10)		•			
29	Pisauridae	HUNT	7.5–40 (23.75)	•	•	•		•
30	Porrhothelidae	BT	30 (30)					•
31	Salticidae	HUNT	10–20 (15)	•	•		•	
32	Selenopidae	HUNT	20 (20)		•			
33	Sicariidae	HUNT	20 (20)		•			
34	Sparassidae	HUNT	20–50 (35)	•	•	•		•
35	Tetragnathidae	WEB	10–15 (12.5)	•	•			
36	Theraphosidae	HUNT	35–100 (67.5)	•	•	(□)	•	•
37	Theridiidae	WEB	6–11 (8.5)	•	•		•	•
38	Thomisidae	HUNT	10 (10)		•			
39	Trechaleidae	HUNT	10–44 (27)	•	•	•		
	All families		Mean = 20.35 ± 1.83	25	27	9 + (1)	9	10 + (2)

SOURCES:

01: ***Missulena***: Online at https://australianmuseum.net.au/learn/animals/spiders/mouse-spiders/

02: ***Coras, Eratigena, Tegenaria***: McCormick & Polis 1982; Nyffeler & Vetter 2018; Nyffeler & Altig 2020; Nyffeler & Gibbons 2021; this paper (Fig. 4A); dead salamander (presumably an immature fire salamander) found in a *Tegenaria* or *Eratigena* web (Rene Jacob, pers. comm.)

03: ***Callobius***: Walton & Walton 2020

04: ***Katissa, Patrera***: Rojas-Morales & Escobar-Lasso 2013; Delia et al. 2019

05: ***Several genera***: Brooks 2012; Nyffeler & Knörnschild 2013; Nyffeler & Altig 2020; Nyffeler & Gibbons 2021; Online at https://www.youtube.com/watch?v=BtHktiVCS6k

06: ***Atrax, Hadronyche***: Rainbow & Pulleine 1918; McKeown 1952; Keast 1981; Main 1996; Brunet 1998; Online at https://australian.museum/learn/animals/spiders/sydney-funnel-web-spider/ Online at https://www.youtube.com/watch?v=fGZ9jOrVwk0 Online at https://www.gettyimages.ch/detail/video/funnel-web-spider-hunting-and-dragging-dead-lizard-stock-videomaterial/544419430?adppopup=true Online at https://www.dailykos.com/stories/2006/5/19/211723/- Online at https://yr4minibeasts.pbworks.com/w/page/54239775/Spideras

07: ***Trichopelma***, ***Unidentified genus***: Nyffeler & Altig 2020; Quintero-Angel & Carr 2010

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08: ***Clubiona*:** Almeida-Reinoso & Coloma 2012
09: ***Corinna*, *Unidentified genus***: Daza et al. 2008; Sabagh et al. 2020
10: ***Several genera***: Nyffeler & Vetter 2018; Nyffeler & Altig 2020; Nyffeler & Gibbons 2021
11: ***Unknown genus***: Online at https://en.wikipedia.org/wiki/Ctenizidae
12: ***Aptostichus***: Wehtje 2007
13: ***Deinopis***: This paper (Fig. 4C)
14: ***Desis***: Nyffeler & Pusey 2014
15: ***Argyroneta:*** Nyffeler & Pusey 2014
16: ***Diplura, Linothele***: Vollrath 1978; Paz 1988
17: ***Eresus:*** Ergashev 1979
18: ***Filistata***: Internet source (see Nyffeler & Gibbons 2021)
19: ***Unidentified genus***: Gopi Sundar 1998
20: ***Cyclocosmia, Ummidia***: Online at http://www.desertmuseum.org/books/nhsd_trapdoor_spider.php
21: ***Gaius, Idiosoma***: Butler & Main 1959; Main 1996
22: ***Linyphia:*** Gudger 1931
23: ***Agroeca:*** Nyffeler & Pusey 2014
24: ***Several genera***: Nyffeler & Pusey 2014; Nyffeler & Altig 2020; Nyffeler & Gibbons 2021
25: ***Miturga:*** Nyffeler & Altig 2020
26: ***Nephila, Nephilingis, Trichonephila***: Brooks 2012; Filipiak & Lewis 2012; Nyffeler & Knörnschild 2013; Nyffeler & Altig 2020; Nyffeler & Gibbons 2021
27: ***Peucetia***: Internet source (see Nyffeler & Gibbons 2021)
28: ***Pholcus, Smeringopus, Unknown genus***: Ackermann 2012; Nyffeler & Gibbons 2021;
Online at https://nationalmuseumpublications.co.za/daddy-long-legs-spider-eats-a-lizard/
Online at https://www.inaturalist.org/observations/15193547
29: ***Several genera***: Zimmermann & Spence 1989; Nyffeler & Pusey 2014; Baba et al. 2019; Nyffeler & Altig 2020; Nyffeler & Gibbons 2021
30: ***Porrhothele:*** Nyffeler & Vetter 2018; Online at https://blog.tepapa.govt.nz/2019/12/17/new-zealands-most-popular-spiders-of-the-decade-surfing-the-spiderverse/
31: ***Hyllus, Paraphidippus, Phidippus***: Nyffeler et al. 2017a, 2021
32: ***Unidentified genus***: The Spider Club of South Africa 33(1):201 [Photo by Marieke de Swart, Pretoria]
33: ***Sicarius***: Ramires & Fraguas 2004; Taucare-Rios & Piel 2020
34: ***Several genera***: Warren 1923; Formanowicz et al. 1981; Henschel 1990; Hamidy et al. 2010; Tanaka 2013; Nyffeler & Pusey 2014; Nyffeler & Gibbons 2021
35: ***Meta, Tetragnatha***: Pastorelli & Laghi 2007; Chatfield et al. 2014
36: ***Several genera***: Nyffeler & Knörnschild 2013; Nyffeler & Vetter 2018; Nyffeler & Altig 2020; Nyffeler & Gibbons 2021
37: ***Several genera***: Brooks 2012; Nyffeler & Vetter 2018; Nyffeler & Altig 2020; Nyffeler & Gibbons 2021
38: ***Thomisus***: Wood 2017
39: ***Cupiennius*, *Trechaleoides, several other genera***: Zina & Gonzaga 2006; Hernández-Cuadrado & Bernal 2009; Gaiarsa et al. 2012; Nyffeler & Pusey 2014; Folt & Lapinski 2017; Nyffeler & Gibbons 2021

one species capable of killing small vertebrate prey (Table 1). In 37 spider families, predation on vertebrates has been witnessed under natural conditions, whereas in the case of two families – the water spider *Argyroneta aquatica* (Clerck, 1757) (Dictynidae) and the intertidal spider *Desis marina* (Hector, 1877) (Desidae) – evidence is based exclusively on laboratory studies (Nyffeler & Pusey 2014). These latter species have been observed to be fish predators when confined with small fish in aquaria, and captive *A. aquatica* have been documented to feed on small frog tadpoles (see Nyffeler & Pusey 2014). The venom of *Argyroneta aquatica* does contain toxins that were shown to effectively target vertebrate nervous systems (Uzenbaev & Lyabzina 2009), suggesting that this spider most likely preys on small aquatic vertebrates under natural conditions as well. The same might be true in *Desis marina* although this has not yet been investigated.

We recognized two groups of vertebrate-eating spiders, namely those that are habitually engaged in vertebrate predation (i.e., "habitual vertebrate-eaters"), and those that feed on vertebrates only occasionally (i.e., "occasional vertebrate-eaters"). In the following, the two groups will be examined comparatively.

3.3 Habitual vertebrate-eaters vs. occasional vertebrate-eaters.—There is compelling evidence that spiders representing ten families are habitually engaged in vertebrate predation. This group includes the Araneidae, Atracidae, Ctenidae, Lycosidae, Nephilidae, Pisauridae, Theraphosidae, Theridiidae, Trechaleidae, and Sparassidae (Fig. 1). The assignment of these ten families to the group of habitual vertebrate-eaters is based on the fact that together they represent 91% of all recorded incidents of vertebrate predation (Fig. 1). The atracids were included in the group of habitual vertebrate-eaters despite the fact that the number of vertebrate prey records available for this family was not as high ($n = 20$ records; Fig. 1) as in the other families from this group ($n > 40$ records; Fig. 1). Including the atracids is justified by the fact that countless frog bones have been detected in the funnels of the northern tree-dwelling funnel-web spider *Hadronyche formidabilis* (Rainbow, 1914) in New South Wales, Australia. These were not taken into account in Fig. 1 because it remained unclear how many frog speciments these bones represented. Be that as it may, the information presented by McKeown (1952) strongly suggests that at least this particular atracid species is predominantly a frog eater. With regard to their phylogenetic origins, the ten families can be assigned to three taxonomic groups: the RTA clade (i.e., families Ctenidae, Lycosidae, Pisauridae, Trechaleidae, and Sparassidae), the Araneoidea clade (i.e., families Araneidae, Neph-

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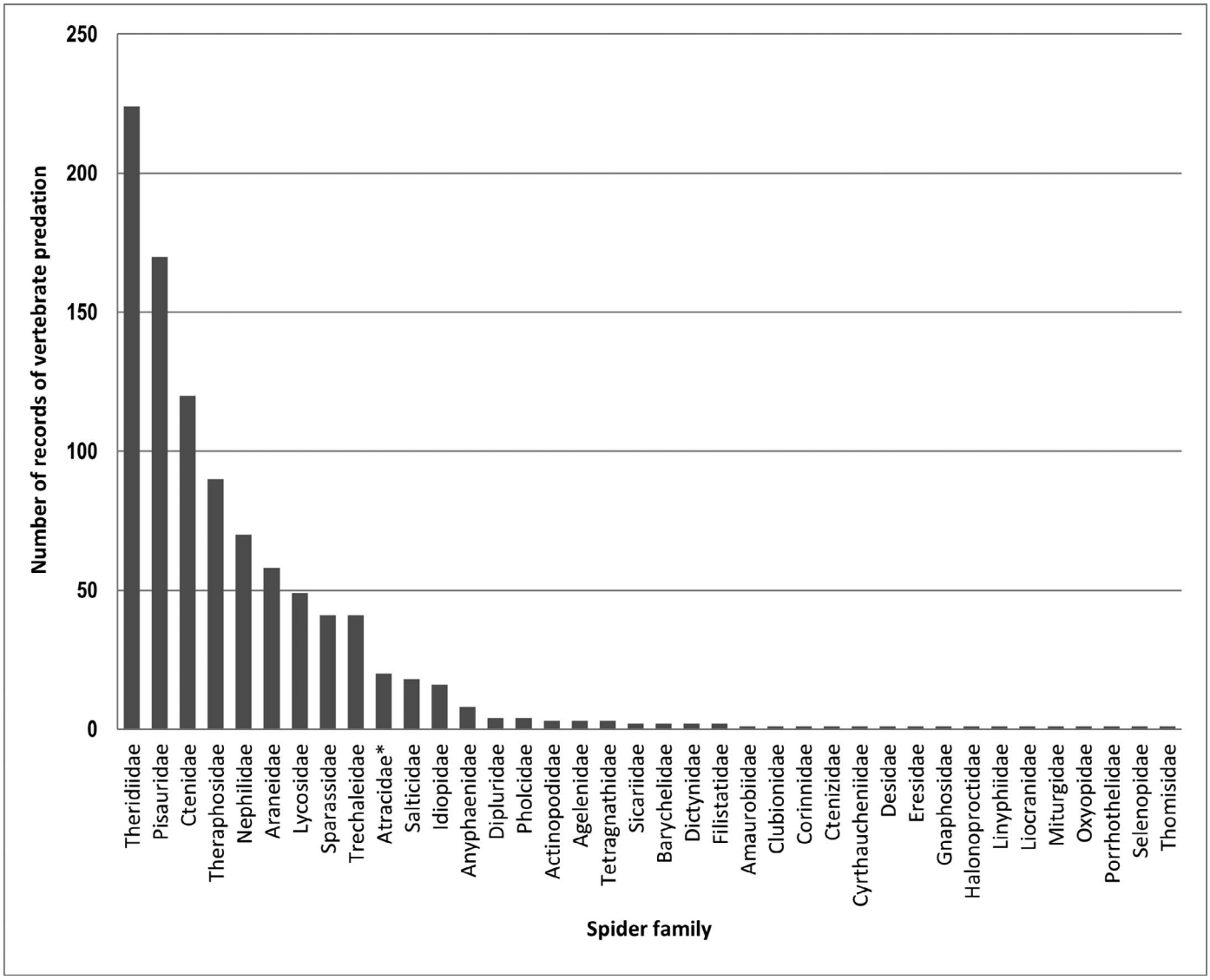


Figure 1.—Frequency distribution of 39 spider families engaged in vertebrate predation based on cummulative literature data (source: McCormick & Polis 1982; Brooks 2012; Nyffeler & Knörnschild 2013; Nyffeler & Pusey 2014; Nyffeler et al. 2017a, 2021; Nyffeler & Vetter 2018; Weisberger 2019; Nyffeler & Altig 2020; Reyes-Olivares et al. 2020; Fulgence et al. 2021; Nyffeler & Gibbons 2021, 2022; Google Scholar & Google Picture Survey for Sparassidae feeding on vertebrates 2021). The ten spider families Atracidae, Theridiidae, Pisauridae, Ctenidae, Theraphosidae, Nephilidae, Araneidae, Lycosidae, Sparassidae, and Trechaleidae are the most prominent vertebrate-eaters (combined 91% of a total of 966 recorded incidents). *The number of records for Atracidae ($n = 20$) presented here is an underestimate [The atracid *Hadronyche formidabilis* must be considered to be a habitual frog-eater due to the fact that countless frog bones had been found in funnels of this species which not could be taken into account in this graph (McKeown 1952)].

ilidae, and Theridiidae), and the mygalomorphs (i.e., families Atracidae and Theraphosidae). Spider species that habitually consume vertebrate prey tend to be large-sized (mean body length = 30.30 ± 4.93 mm, median = 27.00 mm; Tables 1, 2). Examples of spider taxa that habitually prey on vertebrate prey are depicted in Fig. 2.

A second group of spider families is also engaged in vertebrate predation, but vertebrate-eating has been reported to occur only occasionally. This group (made up of the 28 families Actinopodidae, Agelenidae, Amaurobiidae, Anyphaenidae, Barychelidae, Clubionidae, Corinnidae, Ctenizidae, Cyrtaucheniidae, Deinopidae, Desidae, Dipluridae, Eresidae, Filistatidae, Gnaphosidae, Haplonoproctidae, Linyphiidae, Liocranidae, Miturgidae, Oxyopidae, Pholcidae, Porrhothelidae, Salticidae, Selenopidae, Sicariidae, Sparassidae, Tetragnathidae, and Thomisidae) accounts for < 10% of all recorded incidents of vertebrate predation (Fig. 1). Spider species that occasionally consume vertebrate prey tend to be medium-sized (mean = 16.54 ± 1.32 mm; median = 15 mm; Tables 1, 2). Representatives of this latter group are depicted in Figs. 4–6.

In most of the spider families engaged in habitual vertebrate-eating, this type of feeding behavior has a wide global distribution, whereas in the group of occasional vertebrate-eaters this behavior was found to be less widespread; the difference in the mean number of geographic

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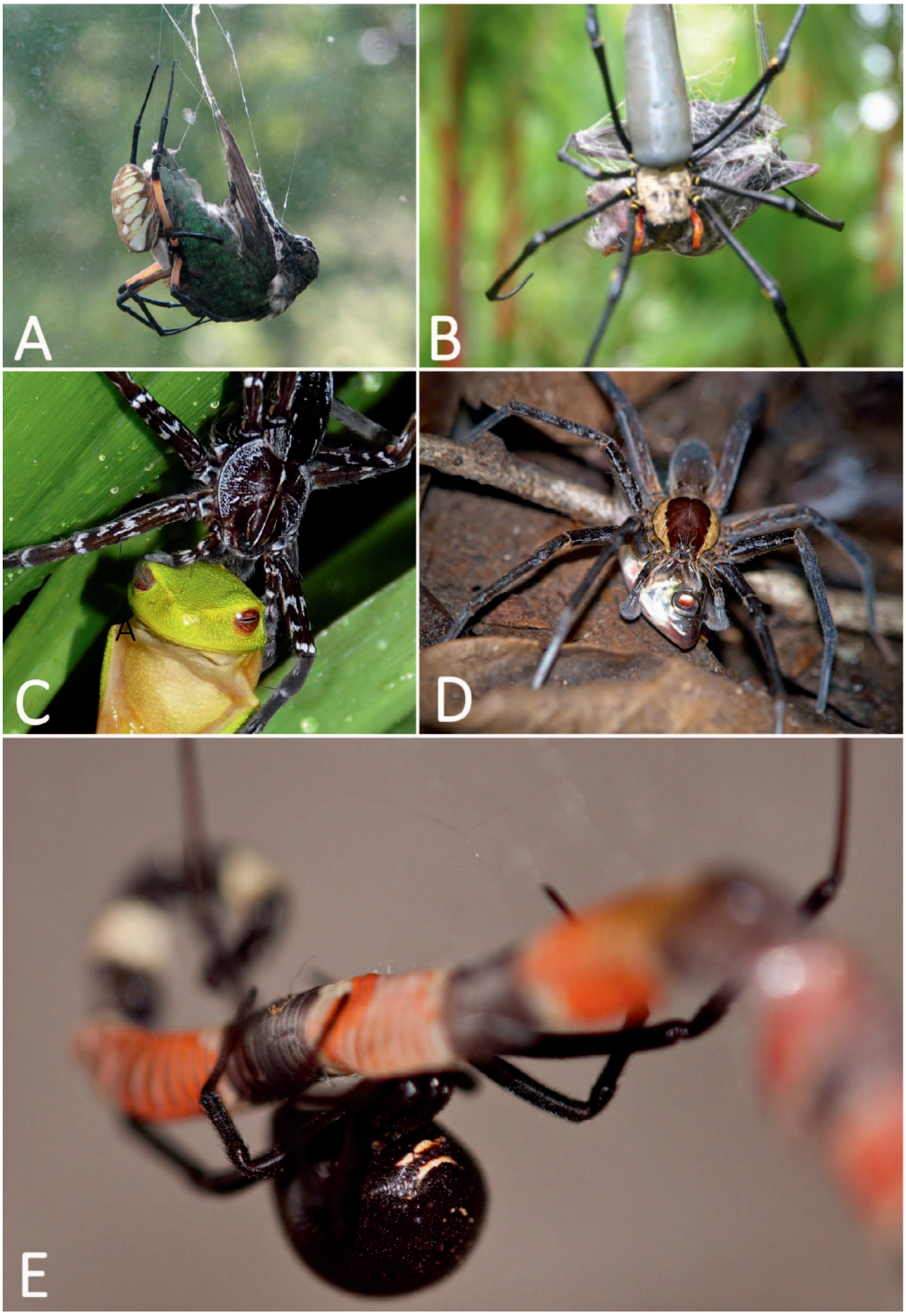


Figure 2.—Examples of habitually vertebrate-eating spiders – **A.** *Argiope aurantia* Lucas, 1833 feeding on a female ruby throated hummingbird (*Archilochus colubris*) in front of a house in College Station, Texas (Photo by Donell S. Frank). **B.** *Nephila pilipes* (Fabricius, 1793) feeding on a small bat (superfamily Rhinolophoidea) entangled in the spider's web; incident observed at the top of the Cockatoo Hill near Cape Tribulation, Queensland, Australia (Photo by Carmen Fabro). **C.** *Megadolomedes australianus* (L. Koch, 1865) (Pisauridae) feeding on a Graceful Tree Frog (*Litoria gracilenta*) in Barratt Creek, Queensland, Australia (Photo by Barbara Maslen "Wild Wings & Swampy Things Nature Refuge, Daintree"). **D.** Adult male of *Ancylometes* sp.(possibly *Ancylometes rufus* (Walckenaer, 1837)) caught a characiform fish (*Cyphocharax* sp.) near Samona Lodge, Cuyabeno Wildlife Reserve, Ecuador (Photo by Ed Germain, Sydney). **E.** Adult female black widow (*Latrodectus hesperus*) feeding on a subadult coral snake *Micruroides euryxanthus* (Elapidae) near the Boyce Thompson Arboretum, Superior, Arizona, USA (Photo by Lawrence L. C. Jones).

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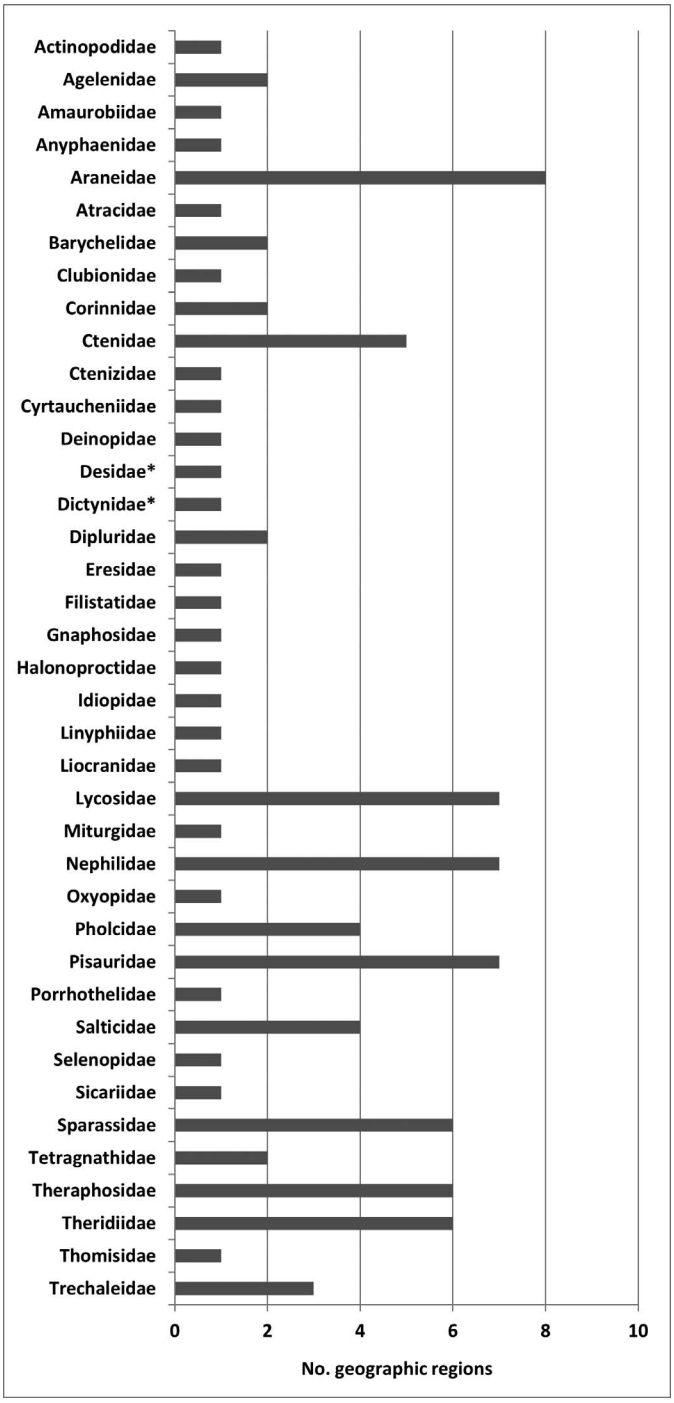


Figure 3.—The number of major geographic regions from which a particular spider family was reported to engage in vertebrate predation (referring to the following nine regions: Europe, Africa, Asia, Australia, North America, Central America, South America, the Caribbeans, and Antarctica). Families followed by * were investigated under laboratory conditions only.

regions was statistically significant (Mann-Whitney U test, $n_1 = 10$, $n_2 = 28$, $Z = -4.59123$, $P < 0.0001$; Table 2). Furthermore, the habitually vertebrate-eating spider families had a significantly more diverse diet (in terms of the number of different vertebrate prey categories included in each spider family's diet) compared with the occasional vertebrate-eaters (Mann-Whitney U test, $n_1 = 10$, $n_2 = 28$, $Z = -3.97796$, $P < 0.0001$; Table 2).

The status of several spider families as vertebrate-eaters is still undecided. For instance, Australian idiopids and the Floridian jumping spider *Phidippus regius* C. L. Koch, 1846 may eventually be determined to be habitual vertebrate-eaters as both have repeatedly been reported to feed on small vertebrates (see McKeown 1952; Butler & Main 1959; Main 1996; Nyffeler et al. 2017a, 2021). Nevertheless, in this paper the idiopids were not assigned to either group, and salticids were assigned to the occasional vertebrate-eaters because of a lack of sufficient quantitative data on these two spider families' natural diets (see Appendix 1). The same applies to some anyphaenid species in the genera *Katissa* Brescovit, 1997 and *Patrera* Simon, 1903. Neotropical anyphaenids have repeatedly been observed to devour eggs/embryos of glass frogs (Centrolenidae) suggesting that these spiders might be habitual predators of frog eggs (see Nyffeler & Gibbons 2022; Fig. 5). In the present study, the anyphaenids were assigned to the occasional vertebrate-eaters because of insufficient evidence. Many more extensive quantitative investigations on the feeding habits of spiders from these last mentioned families are needed before their status as habitual or occasional vertebrate-eaters can unambiguously be determined.

4. DISCUSSION

4.1 Prey-capture adaptations of the habitual vertebrate-eaters.—The ten spider families considered to be habitual vertebrate-eaters (Fig. 1) appear to be adapted to the capture of vertebrate prey in a number of different ways (see McCormick & Polis 1982). The most important prey capture adaptations are (1) sufficient physical strength coupled with large body size, (2) the use of potent venoms, and (3) the use of prey-catching webs (Escoubas & Rash 2004; Lüddecke et al. 2022). Taking into account that vertebrates usually are large, bulky prey compared to the size of their spider attackers, a certain physical strength coupled with large enough body size is a prerequisite for spiders capable of subduing vertebrates (Escoubas & Rash 2004). Indeed the habitual vertebrate-eaters are, on average, significantly larger than the occasional vertebrate-eaters (Table 2; Mann-Whitney U test, $n_1 = 10$, $n_2 = 28$, $Z = -2.86745$, $P < 0.01$). This is illustrated by the examples of the goliath birdeater *Theraphosa blondi* (Latreille, 1804) (Theraphosidae), the giant huntsman spider *Heteropoda maxima* Jäger, 2001 (Sparassidae), and the giant fishing spider *Ancylometes rufus* (Walckenaer, 1837) (Ctenidae) – three habitual vertebrate-eaters belonging to the world's largest spiders. An exception to the rule are the widow spiders (*Latrodectus spp.*; Theridiidae) as well as other members of the theridiid family, which habitually kill and devour vertebrate prey despite the fact that they are of only small to moderate size (usually ~9–13 mm in the case of the widow spiders; Fig. 2E; Table 1). The smallest theridiid witnessed killing and eating a tiny hatchling lizard had a body length of only 3 mm (Welter & Fauth 1996). The widow spiders compensate for their smaller size by constructing webs of extreme stickiness and extraordinary strength and by their use of a highly potent vertebrate-specific toxin (see below).

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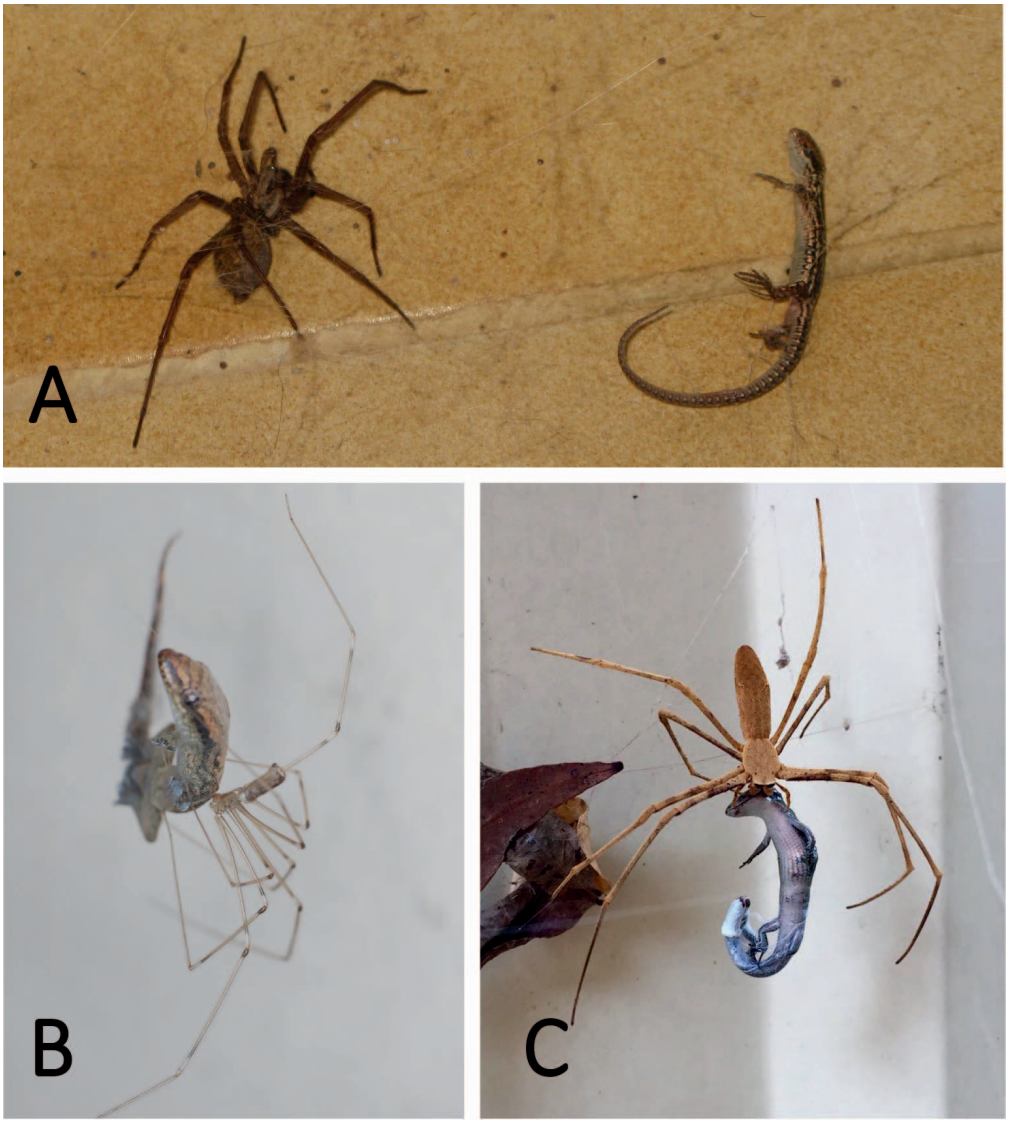


Figure 4.—Examples of occasional vertebrate-eaters – **A.** *Eratigena* sp. (Agelenidae) killed a lizard (*Podarcis muralis*; Lacertidae) in its web in a building in Annepont / Charente Maritime, France (Photo by Vincent Albouy). **B.** *Lepidodactylus lugubris* (Gekkonidae) trapped and killed in a web of *Pholcus phalangioides* (Fuesslin, 1775) after escaping from a terrarium; the incident took place in a building in Switzerland (Photo by Gordon Ackermann). **C.** Net-casting spider *Deinopis subrufa* L. Koch, 1878 (Deinopidae) captured a *Lampropholis* sp. skink (Scincidae) in a backyard near Sydney, Australia (Photo by William Shipway, Attribution 2.0 Generic (CC BY 2)).

Another adaptation is the use of potent venom to paralyze and kill small vertebrates. All 39 spider families engaged in vertebrate-eating (Fig. 1; Table 1) are equipped with venom glands and they all use venom to immobilize their prey (Foelix 2011; Lüddecke et al. 2022). Some unique properties specifically targetting vertebrate nervous systems have been detected in the venoms of at least seven prominent spider families engaged in vertebrate-eating (atracids, ctenids, lycosids, pisaurids, theraphosids, theridiids, and trechaleids (see Herzig & Hodgson 2009; Wang et al. 2013; Valenzuela-Rojas et al. 2019, among others.)). The best known of the vertebrate-specific neurotoxins is the highly potent α-latrotoxin of the widow spiders (*Latrodectus* spp.; Nyffeler & Vetter 2018).

Still another adaptation is the use of prey-catching webs. Enders (1975) theorized that the use of webs increases the size of prey that spiders can capture. According to our survey (Fig.1), half of the 966 recorded incidents of vertebrate predation were by web-weaving spiders and half by webless species. Only three families – namely the Araneidae, Nephilidae, and Theridiidae – construct webs of high tensile strength (i.e., "high energy absorbing webs" *sensu* Craig 1987) particularly suitable for catching large, bulky prey including small vertebrates and large arthropods. Spiders from these three families construct webs of silks considered to be the toughest known biological materials (Agnarsson et al. 2010; Babb et al. 2017). In addition, these webs contain sticky capture threads whose function is to retain prey long enough to be located and attacked by the spiders (Agnarsson & Blackledge 2009). The exceptionally strong webs of the araneids/nephilids permit the capture of large beetles and cicadas as well as small bats and birds (Figs. 2A–B; McKeown 1952; McCormick & Polis 1982; Brooks 2012; Nyffeler &

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Figure 5.—**A.** *Katissa* sp. (Anyphaenidae) feeding on a glassfrog embryo (*Centrolene savagei*; Centrolenidae) in Pueblo Rico, Risaralda, Colombia (Photo by Jesse Delia, American Museum of Natural History, New York). **B.** Another *Katissa* sp. feeding on glassfrog embryos (*Cochranella resplendens*) in Wawa Sumaco Napo, Ecuador (Photo by Jesse Delia).

Knörnschild 2013), whereas widow spiders (Theridiidae) are capable of trapping large beetles, Jerusalem crickets, scorpions, small snakes, lizards, and even mice and rats (Fig. 2E; Gertsch 1979; Nyffeler & Vetter 2018; Nyffeler & Gibbons 2021).

By means of these types of prey-capture adaptations, habitual vertebrate predators among the spiders are able to not only kill vertebrate prey many times larger and heavier than themselves, they also are able to subdue highly toxic predaceous vertebrates such as Australian brown snakes (*Pseudonaja* spp.), rattlesnakes (*Crotalus* spp.), Neotropical lanceheads (*Bothrops* spp.), and New World coral snakes (*Micrurus* and *Micruroides* spp.; e.g., Fig. 2E; Nyffeler & Gibbons 2021).

4.2 Prey capture behavior of the occasional vertebrate-eaters.—In this paper, spiders from 28 families are considered to be occasional vertebrate-eaters (Figs. 4–6). The spiders from these families had previously not been observed (or very rarely observed) subduing vertebrates. In the case of some of these spiders, involvement in vertebrate predation appears to be unexpected and such species most likely are not adapted to vertebrate predation. The significantly smaller average body size of these spiders suggests that they have reduced physical strength compared with the larger-sized habitual vertebrate-eaters (see above). Also some spider species from this group (e.g., tetragnathids and linyphiids) produce small, feeble webs (i.e., "low energy absorbing webs" *sensu* Craig 1987) not suitable for the interception of vertebrates. The unexpected occurrence of vertebrate predation in spiders of this type might be considered as chance encounters that took place when a tiny vertebrate (eventually weakened by malnutrition or disease) crossed the path of an opportunistic spider. An incident of this type has been documented from South Africa where a crab spider (*Thomisus blandus* Karsch, 1880) overpowered and devoured a tiny Cape dwarf gecko of only ~4.5 cm total length (Fig. 6A–C; Wood 2017).

4.3 How does vertebrate-eating affect the food supply of spiders?—So far only a few quantitative assessments of vertebrates as spider prey exist. In several studies from very different regions of the globe, vertebrates were documented to make up $< 1\%$ of the spiders' total prey (Appendix 1 – Zimmermann & Spence 1989; Henschel 1990; Hodar & Sanchez-Pinero 2002; Szymkowiak et al. 2005; Bryan et al. 2015), whereas in many other published dietary studies vertebrates were not even present in spider diets (see Nentwig 1987; Nyffeler 1999). A few studies have documented that vertebrates made up a considerable percentage (8–30%) of the total diet (Appendix 1 – McKeown 1952; Lapinski & Tschapka 2013; Baba et al. 2019; Valenzuela-Rojas et al. 2019; Ramírez et al. 2021; pooled data Edwards 1980 / Nyffeler et al. 2021; Wilder & Simpson 2022). These latter studies were based on low prey numbers ($n = 21$–77) and must therefore be interpreted with caution.

Large theraphosids in the genera *Avicularia* Lamarck, 1818, *Grammostola* Simon, 1892, *Lasiodora* C. L. Koch, 1850, *Theraphosa* Walckenaer, 1805, etc. were assumed to feed heavily on frogs and other vertebrates (see Emerton 1926; McCormick & Polis 1982; Hillyard 1994; Nyffeler & Altig 2020; Nyffeler & Gibbons 2021; Rick West, pers. comm.). From a point of view of optimal foraging theory it would make perfect sense if such large spiders (weighing 10–100 g) would feed to a large extent on vertebrate prey since those are usually more profitable food items than most arthropod prey due to their larger body mass (see Nyffeler & Knörnschild 2013; Nyffeler & Pusey 2014). In line with this, the Brazilian tarantula *Grammostola actaeon* (Pocock, 1903) was labeled as a specialized vertebrate-eater in the literature (see Berland 1932; Millot 1949; Gertsch 1979; Hillyard 1994) due to its acceptance of small snakes, frogs, and lizards as prey when offered to it in captivity (see Emerton 1926).

Predation on vertebrates appears to contribute overall rather insignificantly to the food supply of most spiders. But from the perspective of a single individual, opportunistically feeding on a vertebrate prey item may be quite rewarding. The

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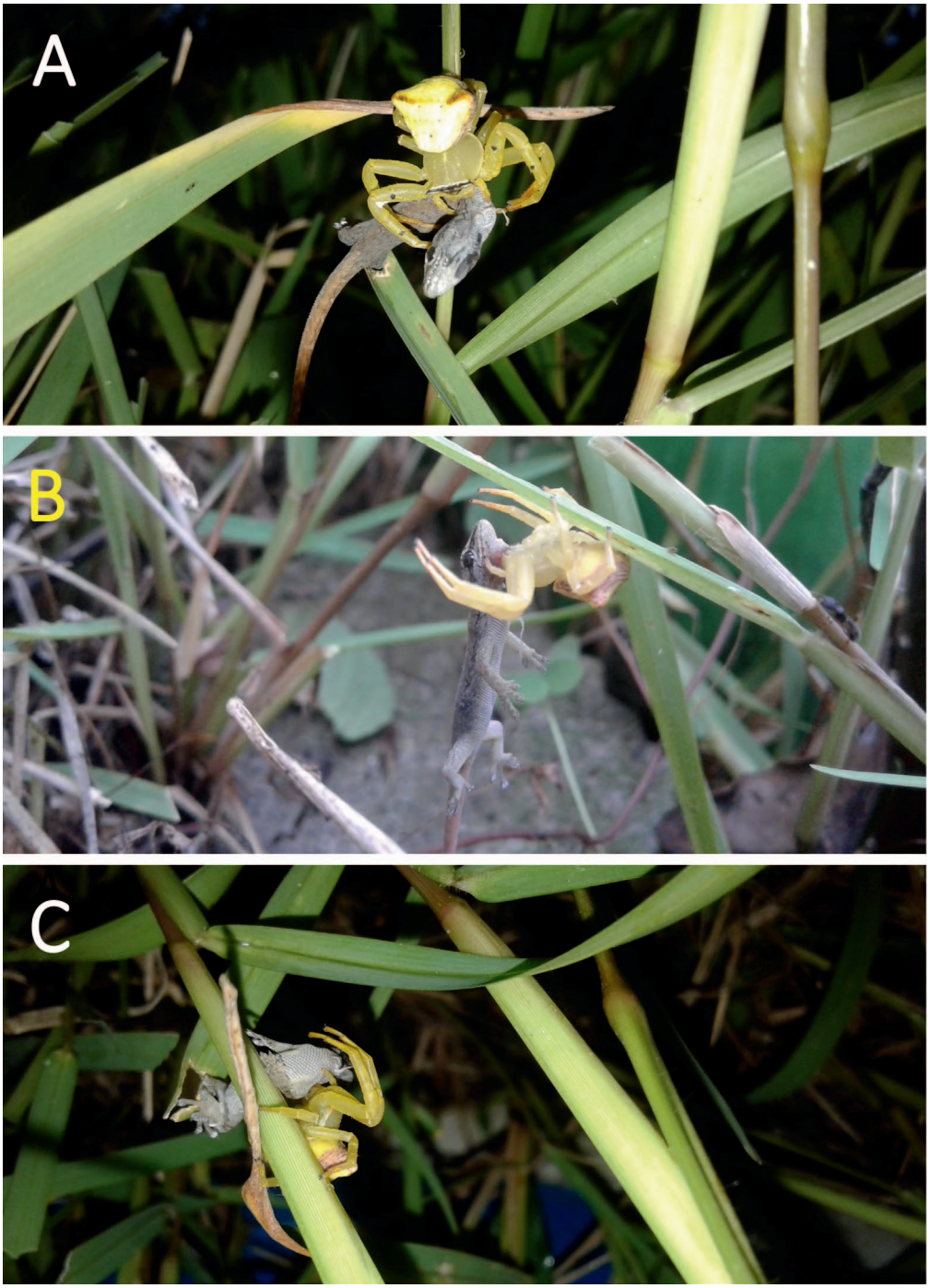


Figure 6.—Another example of an occasional vertebrate-eater – **A–C.** Female *Thomisus blandus* Karsch, 1880 (Thomisidae) consuming a juvenile *Lygodactylus capensis* (Gekkonidae) in a vegetable garden near the Umngazi mouth in the Eastern Cape, South Africa (Photo by Mathew Wood). The gecko was about 4.5 times as long as the spider.

occasional capture of vertebrate prey may be sufficient to fulfill the energetic needs for reproduction, as suggested for large orb-weavers in the "rare, large prey hypothesis" (Nyffeler & Knörnschild 2013). The exceptionally long "handling time" in terms of processing vertebrate prey suggests that spiders can extract an exceptionally large amount of liquified prey biomass from that kind of over-sized prey items (vertebrate prey is often several times larger than the spider itself). While it typically takes 0.5–2 hours to consume an insect prey (M. Nyffeler, pers. obs.), spiders were observed feeding on vertebrate prey for many hours up to several days (see Nyffeler & Knörnschild 2013; Nyffeler & Pusey 2014; Nyffeler & Altig 2020; Nyffeler & Gibbons 2021). Excess food – which is not instantly used for the metabolism – is stored in the form of glycogen and lipids in resorptive cells of the interstitial tissue as an energy reserve (Foelix 2011). In times of

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Table 2.—Comparison of habitual vertebrate-eaters vs. occasional vertebrate-eaters regarding mean spider body length, extent of global distribution, and dietary diversity. The statistical significance of the difference of the mean values for each of the three comparisons was tested using a two-tailed Mann-Whitney *U* test. A 39th family (family Idiopidae) was not included in this comparison because its assignment to either of these two groups of families is still unclear.

	Habitual vertebrate-eaters $n = 10$ spider families	Occasional vertebrate-eaters $n = 28$ spider families	Statistical significance of the difference of the mean
(1) Mean body length (mm)[A]	30.30 ± 4.93 (median = 27.00)	16.54 ± 1.32 (median = 15.00)	$p < 0.01$
(2) Mean number of geographic regions per spider family (= extent of global distribution)[B]	5.60 ± 0.67 (median = 6.00)	1.39 ± 0.16 (median = 1.00)	$p < 0.0001$
(3) Mean number of vertebrate prey categories per spider family (= dietary diversity) [A]	4.00 ± 0.15 (median = 4.00)	1.29 ± 0.11 (median = 1.00)	$p < 0.0001$

Data taken from [A]Table 1, [B]Figure 3.

low food availability, the spiders can then draw on these energy reserves, which allows them to bridge longer periods of hunger. However, oftentimes a spider will eat only a small portion of a dead vertebrate. What is left is later consumed by scavengers (ants, wasps, flies, molds) and returned to the natural cycle of nutrients.

5. CONCLUDING REMARKS

Our survey unveiled a larger number of vertebrate-eating spider species from families previously not anticipated to prey on vertebrates. Interestingly, 16 (= 41%) of the total of 39 spider families documented to be engaged in vertebrate predation are known to also occasionally feed on earthworms and/or gastropods, implying that many spider taxa have a more diverse diet than previously thought (see Nyffeler & Symondson 2001; Nyffeler et al. 2001; Nyffeler et al. 2017b). The capability of spiders to supplement their usual arthropod diets with different types of alternative food might be of nutritional significance, most notably during periods of food scarcity (also see Nyffeler et al. 2016, 2017b). The findings presented here improve our general understanding of spider feeding ecology and provide a first assessment of the contribution of vertebrate prey as an alternative food source.

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Appendix 1.—Percentage of vertebrates in the natural diet of representative spider species (literature survey). n = total number of prey items. Arranged in ascending order of the percentages of vertebrates in the total diet.

Spider species / family	Type of vertebrate prey	Geographic area	% vertebrates in total diet	Reference
Latrodectus hasselti Thorell, 1870 / Theridiidae	Squamata	New Zealand	0.06[A] [$n = 1786$]	Bryan et al. 2015
Dolomedes triton (Walckenaer, 1837) / Pisauridae	Anura	Alberta, Canada	0.16[A] [$n = 625$]	Zimmermann & Spence 1989
Argiope bruennichi (Scopoli, 1772) / Araneidae	Anura	Poland	0.23[A] [$n = 430$]	Szymkowiak et al. 2005
Leucorchestris arenicola Lawrence, 1962 / Sparassidae	Squamata	Namib desert, Africa	0.3[A] [$n = 377$]	Henschel 1990
Latrodectus lilianae Melic, 2000 / Theridiidae	Squamata	Spain	0.3[A], ~1.2[B] [$n = 1267$]	Hódar & Sanchez-Pinero 2002
Phoneutria boliviensis (F. O. Pickard-Cambridge, 1897) / Ctenidae	Squamata	Colombia	0.85[A] [$n = 234$]	Ramírez et al. 2021
Ctenidae and Trechaleidae	Anura, Squamata, Pisces	Costa Rica	7.7[A] [$n = 52$]	Lapinski & Tschapka 2013
Latrodectus hasselti / Theridiidae	Squamata	Australia	8.0[A] [$n = 77$]	Wilder & Simpson 2022
Phoneutria boliviensis (F. O. Pickard-Cambridge, 1897)	Anura, Squamata	Colombia	14.3[A] [$n = 21$]	Valenzuela-Rojas et al. 2019
Latrodectus hasselti / Theridiidae	Squamata	Australia	17.0[B] [$n = 77$]	Wilder & Simpson 2022
Phidippus regius C. L. Koch, 1846 / Salticidae	Anura, Squamata	Florida, USA	29.5[A] [$n = 44$]	Pooled data from Edwards 1980 [$n = 31$]; Nyffeler et al. 2021 [$n = 13$]
Dolomedes orion Tanikawa, 2003 / Pisauridae	Anura, Squamata	Japan	30.4[A] [$n = 23$]	Baba et al. 2019
Hadronyche formidabilis (Rainbow, 1914) / Atracidae	Anura	Australia	Frogs made up the bulk of the diet[C] [$n = ?$]	McKeown 1952

[A] % based on prey numbers. [B] % based on prey biomass. [C] % based on prey biomass during the summer months.

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