Erratum

Source: The Journal of Arachnology, 49(3) : 415

Published By: American Arachnological Society

URL: https://doi.org/10.1636/JoA-S-21-300

2021. Journal of Arachnology 49:1–27

INVITED REVIEW

Spiders (Arachnida: Araneae) feeding on snakes (Reptilia: Squamata)

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Abstract. In this paper, 319 incidents of snake predation by spiders are reported based on a comprehensive global literature and social media survey. Snake-catching spiders have been documented from all continents except Antarctica. Snake predation by spiders has been most frequently documented in USA (51% of all incidents) and Australia (29%). The captured snakes are predominantly small-sized with an average body length of 25.9 ± 1.3 cm (median = 27 cm; range: 5.8–100 cm). Altogether >90 snake species from seven families have been documented to be captured by >40 spider species from 11 families. About 60% of the reported incidents were attributable to theridiids (≈0.6–1.1 cm body length), a spider family that uses strong tangle webs for prey capture. Especially the Australian redback spider (*Latrodectus hasselti* Thorell, 1870), the African button spider (*Latrodectus indistinctus* O. Pickard-Cambridge, 1904), an Israeli widow spider (*Latrodectus revivensis* Shulov, 1948), and four species of North American widow spiders (*Latrodectus geometricus* C.L. Koch, 1841, *Latrodectus hesperus* Chamberlin & Ivie, 1935, *Latrodectus mactans* (Fabricius, 1775), and *Latrodectus variolus* Walckenaer, 1837) – equipped with a very potent vertebrate-specific toxin (α-latrotoxin) – have proven to be expert snake catchers. The use of vertebrates as a supplementary food source by spiders represents an opportunity to enlarge their food base, resulting in enhanced survival capability. Interestingly, the snakes captured by spiders also encompasses some species from the families Elapidae and Viperidae known to be highly toxic to humans and other vertebrates. Not only do spiders sometimes capture and kill snakes, quite often the tables are turned – that is, a larger number of arthropod-eating snake species (in particular nonvenomous species in the family Colubridae) include spiders in their diets.

Keywords: Araneae, Serpentes, black widow, *Latrodectus*, Theraphosidae, predation, intraguild predation, venomous spiders, venomous snakes

https://doi.org/10.1636/JoA-S-20-050

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1. INTRODUCTION

Spiders are among the most common and abundant predators in terrestrial ecosystems (Coddington & Levi 1991; Nyffeler & Sunderland 2003). With >49,000 described species, these animals exhibit an enormous diversity of lifestyles and foraging strategies (Nyffeler & Birkhofer 2017; World Spider

Catalog 2020). While spiders had been believed for a long time to depend almost exclusively on live insects or other small arthropods for food, it has been shown in more recent years that the spiders' feeding habits are much more diverse than previously thought. The natural diets of the spiders include "odd foods" such as earthworms (Annelida), velvet worms (Onychophora), bristle worms (Polychaetes), slugs (shell-less Gastropoda), snails (shelled Gastropoda), amphipods (Talitridae), shrimps (Palaemonidae), crayfish (Cambaridae), freshwater crabs (Trichodactylidae), and a large variety of different types of plant materials (Nyffeler & Symondson 2001; Nyffeler et al. 2001, 2016, 2017b). Furthermore, spiders capture a variety of small vertebrates 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) (see Nyffeler & Altig 2020).

Snakes are occasionally overpowered and eaten by a limited number of spider taxa (i.e., ophiophagy; McCormick & Polis 1982). Although ophiophagy in spiders is well documented (e.g., Emerton 1926; Pinkus 1932; McCormick & Polis 1982; Raven & Gallon 1987; Punzo & Henderson 1999), a synthesis focusing on this specific topic has not yet been published. Here, we compile and review all that is currently known on snake predation by spiders.

2. METHODS

2.1 Data collection.—We searched published reports on snake predation by spiders with 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. We made a library search of books and scientific journals not included in the large databases. A total of 319 reports of predation (or predation attempts) on snakes by spiders were found, about 1/3 of which had previously been published in the scientific literature (see Supplementary Table S1, online at https://doi.org/10.1636/JoA-S-20-050.s1). The remaining 2/3 were found on social media sites (e.g., Scientific American, National Geographic, Australian Geographic, BBC, YouTube, Project Noah, and Panama Birds & Wildlife; see Supplementary Table S1) or provided to us as personal communication by scientists/photographers. Of the 319 records, 297 (93%) refer to naturally occurring incidents witnessed in the field or in buildings; the remaining 22 records (7%) are based on laboratory feeding trials or staged field experiments. In one case where it was stated that a certain type of predation event had been witnessed several dozen times (without providing an exact number; Peters 2016), we hypothetically estimated that this type of predation event had occurred two dozen times (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 snakes depicted in photos.—Almost 80% of the 319 reported predation events were documented with photos or videos. Some photos or videos depicted unidentified spiders and/or snakes which were identified to the lowest taxon possible on our behalf by established spider and snake taxonomists. Spiders were identified by R. Bennett, A. Dippenaar-Schoeman, G.B. Edwards, H. Höfer, P. Jäger, K. Kissane, Y. Lubin, R. Raven, B. Thaler-Knoflach, and R. West. Snake identifications were carried out by W. Gibbons, W. Lamar, R. Shine, S. Spawls, G. Vogel, and R. Whitaker. Some snakes unable to be unambiguously identified (based on only photos) are indicated in Appendix 2 by a question mark behind the snake's name, but the cumulative data provide an estimate of the number of snake morphospecies preyed on by spiders.

Several reports from the northeastern part of USA (Vermont, Connecticut, Maryland, Pennsylvania, and New York) or the southeastern part of Canada (Ontario) of unidentified theridiids killing snakes in a manner typical of black widows are from a geographic area that coincides with the geographic range of *Latrodectus variolus* Walckenaer, 1837 (see https://usaspiders.com/latrodectus-variolus-northern-black-widow/) suggesting that in some of these cases, the predator in question was most likely the northern black widow *Latrodectus variolus*.

Snake and spider nomenclatures are based on Uetz et al.'s "The Reptile Database – update from 2020" and the "World Spider Catalog 2020", respectively. In 89% cases, at least a family-level identification of the reported snake victims could be conducted, whereas 11% remain unidentified. Contrary to the "World Spider Catalog 2020", we placed the genera *Nephila* Leach, 1815 and *Trichonephila* Dahl, 1911 in the family Nephilidae (sensu Kuntner et al. 2019).

Body length of spiders is understood as the length of cephalothorax + abdomen (without legs). Snake body length is defined as total length (= snout-vent length + tail length). In cases where information of spider body length was missing in published reports, average spider body length values representative of those species, extracted from arachnology books, were added to the data set in the Supplementary Table S1. So, for instance, an average spider body length value of 1.0 cm was assumed for adult female black widows (*Latrodectus* spp.). Spider body length data used in this paper are biased towards the araneomorph spiders (i.e., in particular the small-sized theridiids) due to the fact that in many reports referring to the much larger-sized mygalomorphs body length data were unavailable. Furthermore, because mygalomorph species show wide intraspecific variation in body size, it was usually not possible for this spider group to operate with an assumed species-specific body length value based on arachnology books. In very few cases, where exclusively snout-vent length data for snakes were available, those were converted to total length data, using conversion factors taken from the literature (Boada et al. 2005; Brust 2013; Mirtschin et al. 2017; Murphy et al. 2019).

Based on snake body length information, corresponding snake body mass values have been roughly estimated based on published snake length/body mass ratios (see Nyffeler et al. 2017a) if snake body mass was not provided in the published predation accounts.

2.3 Definition of the term "venomous spiders".—All spider species except for the uloborids and the holarchaeids possess a pair of venom glands and are therefore capable of producing venoms used for prey capture and in some cases also for defense (Coddington & Levi 1991; Foelix 2011). A limited number of notoriously dangerous spiders are referred to as "venomous spiders" (Bücherl & Buckley 1971). This group of spiders includes in particular widow spiders (*Latrodectus* spp.), wandering spiders (*Phoneutria* spp.), funnel-web-spiders (*Atrax* spp.), and recluse spiders (*Loxosceles* spp.). The very potent venoms produced by spiders from this group are potentially dangerous not only to humans, they can also be lethal to other mammals, birds, snakes, lizards, anurans, etc. (Nyffeler & Vetter 2018; Nyffeler & Altig 2020).

2.4 Definition of the terms "venomous snakes" vs. "nonvenomous snakes".—Venomous snakes include species of snakes that use their fangs to inject toxins into their victims (Encyclopedia Britannica 2020a). In this paper, the term venomous snakes is used for species known to be potentially lethal to humans; included in this category are the families Elapidae and Viperidae. The toxicity of various snake species is compared based on LD_{50} values of snake venom injected in mice. In contrast, nonvenomous snakes are species that do not produce a toxin that is clinically significant to humans. Nonvenomous snakes are represented by the families Colubridae, Dipsadidae, Lamprophiidae, Leptotyphlopidae, and Typhlopidae.

2.5 Definition of the term "poisonous snakes".—By definition the term "venomous snakes" implies that these snakes inject toxins by biting their prey or enemy, while the term "poisonous snake" is applied when a snake is toxic for a natural enemy after being eaten by it (Encyclopedia Britannica 2020b). A snake species potentially poisonous to spiders is the common garter snake (*Thamnophis sirtalis*). This snake can become poisonous to its natural enemies after preying on toxic newts (Williams et al. 2004).

2.6 Statistical methods.—In this paper, neither spider body length data nor snake body length data are normally distributed (tested with the Shapiro-Wilk test software, online at http://www.statskingdom.com/320ShapiroWilk.html). Likewise, LD_{50} data for spiders and snakes are not normally distributed (Shapiro-Wilk test). Accordingly, the median must be used as a measure of central tendency. Despite the fact that data from field collections and observations are often not normally distributed, many authors still use the mean as central tendency. In order to make our data comparable to those from the literature, we calculated a mean ($\pm$ SE) in addition to the median (while at the same time acknowledging that this is not the ideal measure). The two-tailed Mann-Whitney *U* test was used to compare mean snake lengths in USA vs. Australia, and the same test was also used to compare mean LD_{50} values (mg/kg mouse) for venomous spiders vs. venomous snakes. These analyses were performed at https://www.socscistatistics.com/tests/mannwhitney/default2.aspx. To test whether the percentages of rescued snakes vs. rescued birds differed statistically significantly, a chi-square calculator test (without Yates's correction) was performed; this was accomplished using MedCalc statistical software (online at https://www.medcalc.org/calc/comparison_of_proportions.php). This same statistical test was also performed to test whether there was a significant difference between the percentages of venomous snakes killed on different continents. Based on 86 available data pairs, snake body lengths and spider body lengths were tested for a relationship using the Pearson Correlation Coefficient Calculator (online at https://www.socscistatistics.com/tests/pearson/).

3. RESULTS

3.1 Which spider species are engaged in snake predation?—More than 30 spider species have been reported to prey on snakes under natural conditions, and 11 additional species have been documented to capture and eat snakes in captivity or in staged field experiments (Table 1 and Appendix 1). The following ten families have been documented to be engaged in snake predation under natural conditions: Agelenidae, Araneidae, Ctenidae, Idiopidae, Nephilidae, Pholcidae, Pisauridae, Sparassidae, Theraphosidae, and Theridiidae (Table 1 and Appendix 1). Additionally, a large-sized species of the wolf spider family (Lycosidae) has been witnessed attacking a snake in captivity (Anonymous 2014). Based on available data, snake-eating spiders had an average body length of 1.69 $\pm$ 0.19 cm (median = 1.00 cm, $n = 86$).

Approximately 60% of the 319 incidents of snake predation were attributable to theridiids ($\approx$0.6–1.1 cm body length), a spider family that uses strong tangle webs to capture prey (Table 1; Figs. 1–5). Roughly half of all incidents were attributable to widow spiders (*Latrodectus* spp.; Table 1). Several species of widow spiders (*Latrodectus* spp.) have proven to be expert snake catchers (Figs. 1A, 2B, 3–5), including four species of North American widow spiders (*Latrodectus geometricus* C.L. Koch, 1841, *Latrodectus hesperus* Chamberlin & Ivie, 1935, *Latrodectus mactans* (Fabricius, 1775), *Latrodectus variolus* Walckenaer, 1837), the Australian redback spider (*Latrodectus hasselti* Thorell, 1870), the African button spider (*Latrodectus indistinctus* O. Pickard-Cambridge, 1904), an Israeli widow spider (*Latrodectus revivensis* Shulov, 1948), and a white colored, not uniquely identifiable Iranian widow spider (possibly *Latrodectus pallidus* O. Pickard-Cambridge, 1872). The seven widow species reported in our study are of similar size (usually weighing $\approx$0.35–0.50 g as adult females) with maximum weights of up to $\approx$1 g (Canadian Geographic 2006; Nel et al. 2014; Nyffeler & Vetter 2018). Snakes are killed exclusively by adult female widow spiders (see Nyffeler & Vetter (2018) for an explanation).

The second most important snake catchers among the spiders were members of the tarantula family (Theraphosidae) which made up 10% of all instances of snake predation by spiders (Table 1; Figs. 6, 7A). These are large-sized vagrant spiders which do not spin a catching web. Some members of this family hunt prey in trees, while others catch prey on the ground. Tarantulas are among the largest and most powerful spiders, whose largest species reach a leg-span of >20 cm and a weight of up to >100 g (Nyffeler & Knörnschild 2013). Other nonweb-building spiders (e.g., Pisauridae) were less significant snake catchers (Table 1; Fig. 7B).

Large orb-weavers of the families Araneidae and Nephilidae reached third place in terms of importance as snake catchers (8.5% of all incidents, Table 1; Fig. 8). Especially species in the genera *Argiope* Audouin, 1826, *Nephila*, and *Trichonephila*

Table 1.—Spider families engaged in snake predation or predation attempts (based on 319 incidents reported in the scientific literature or in the social media). Evidence based on field observations except for Lycosidae.

Taxon #	Spider family	Number of species within family	Number of predation events	Source
01	Agelenidae	1	1	McCormick & Polis 1982
02	Araneidae	3	10	Anonymous 1911; Pinkus 1932; Burt 1949
03	Ctenidae	2	3	Sasa et al. 2009; Sorokin & Stuckert 2017
04	Idiopidae	1	1	Main 1996
05	Lycosidae[A]	1	1	Anonymous 2014
06	Nephilidae[B]	2	17	Wilder 1865; Zippel & Kirkland 1998; Tanaka & Mori 2000; Jantos 2012
07	Pholcidae[C]	≥1	2	Awford 2016
08	Pisauridae	3	4	Lazcano et al. 2005; Gerald 2006
09	Sparassidae[D]	≥1	3	Parkhill 2020; https://www.youtube.com/watch?v=g3wKiVwfNxs Accessed 5 June 2020; https://www.recordchina.co.jp/b7342-s0-c30-d0000.html Accessed 6 June 2020
10	Theraphosidae	19	33	Emerton 1926; Owens 1949; Punzo & Henderson 1999; Avila & Porfirio 2008; Sasa et al. 2009; Nunes 2010; Borges et al. 2016; Jorge et al. 2016; Pinto et al. 2017; Almeida et al. 2019; Da Silva et al. 2019
11	Theridiidae	11	187	Klauber 1940; Neill 1948; Bush 1961; Newlands 1978; De Rebeira 1981; Orange 1990; Petrov & Lazarov 2000; Tanaka & Mori 2000; Bayliss 2001; De Sousa et al. 2007; Ervin & Carroll 2007; Hall & Johnson 2007; Pruett & Jadin 2010; McGuinness 2013; Beaman & Tucker 2014; Rocha et al. 2017; Stevenson & Crook 2018
–	Unspecified web-spinners	N/A	51	Brown 1895; Swanson 1952; Hutchins 1968; Myers 1974; Groves & Groves 1978; Sanders 1982; Moehn 1984; Bush 1989, Klemens 1993; Faraone et al. 2019; and others
–	N/A	N/A	6	Branch 1998; Linzey & Clifford 2002; Gibbons 2017; and others
Total		≥45	319	

[A] Predation attempt on a snake by a captive *Hogna carolinensis* (Walckenaer, 1805)
[B] *Nephila and Trichonephila* placed in Nephilidae (sensu Kuntner et al. 2019)
[C] Between 1–2 spider species (one incident in Arizona and one in Australia)
[D] Between 1–3 species species (incidents in China, India, and Australia)

have been witnessed preying on snakes that got trapped in their strong orb-webs (Wilder 1865; Gudger 1931; Pinkus 1932; Burt 1949; Zippel & Kirkland 1998; Tanaka & Mori 2000; Jantos 2012). The spiders in the genera *Nephila* and *Trichonephila* spin orb-webs with a diameter of 0.5–1.5 m (Nyffeler & Knörnschild 2013). The largest snake reported as a spider's prey, an adult green snake (*Opheodrys aestivus*) of 75 cm snout-vent length (equaling ≈1 m total length) had been caught in a web of *Trichonephila clavipes* (Linnaeus, 1767) in Florida (Zippel & Kirkland 1998).

These three spider groups (Theridiidae, Theraphosidae, and Araneidae/Nephilidae) combined were responsible for roughly 80% of all reported incidents of snake predation (Table 1).

3.2 Which snake species are captured by spiders?—The snakes known as prey of spiders had an average body length of 25.9 ± 1.3 cm (median = 27 cm; range: 5.8–100 cm; $n = 104$). The vast majority of snake victims were either neonates or juveniles (e.g., Burt 1949; Owens 1949; Klemens 1993; Durigo 2010; Peters 2016) with a rather low body weight (see snake body weights in Table 2 for a comparison). The smallest snakes captured by spiders (i.e., juvenile typhlopids) are known to weigh only 0.2–0.7 g (Table 2). Younger snake individuals are probably more vulnerable to predators than adults due to their small size (Jorge et al. 2016). But on the other hand, in rare cases larger colubrids and vipers captured by spiders were fairly heavy, reaching an estimated body weight of up to 40–60 g (see subsection 3.6). The vast majority of snakes killed by spiders are terrestrial, with some exceptions. For example, there are several reports of juveniles of the northern water snake *Nerodia sipedon* having been killed by web-building spiders (Anonymous 1946; online at https://www.youtube.com/watch?v=l8v8LPgzD_I).

The group of snakes killed and eaten by spiders in the wild encompasses 86 species, representing seven families (i.e., Colubridae, Dipsadidae, Elapidae, Lamprophiidae, Leptotyphlopidae, Typhlopidae, and Viperidae; Table 3, Appendix 2). In addition, 5 more snake species (i.e., *Chironius carinatus*, *Drymobius margaritiferus*, *Imantodes cenchoa*, *Bothrops jararaca*, and *Crotalus durissus*) were killed and consumed by spiders in captivity or during staged field experiments. Two families (Colubridae and Elapidae) accounted for 84% of all 284 identified snake victims, with colubrids being the most representative family (162 incidents, Table 3). The predominance of Colubridae in the total of captured snakes reflects the fact that colubrids are by far the largest and most abundant snake family on all continents except Australia (Degenhardt et al. 2005). The list of North American colubrid snakes known as prey of spiders includes the following species: black-headed and flat-headed snakes (*Tantilla gracilis* and *Tantilla hobartsmithi*), brown snakes (*Storeria dekayi* and *Storeria occipitomaculata*), crayfish snakes (*Regina septemvittata*), earth snakes (*Virginia valeriae*), garter snakes (*Thamnophis cyrtopsis* and *Thamnophis sirtalis*), glossy snakes (*Arizona elegans*), green snakes (*Opheodrys aestivus* and *Opheodrys vernalis*), hog-

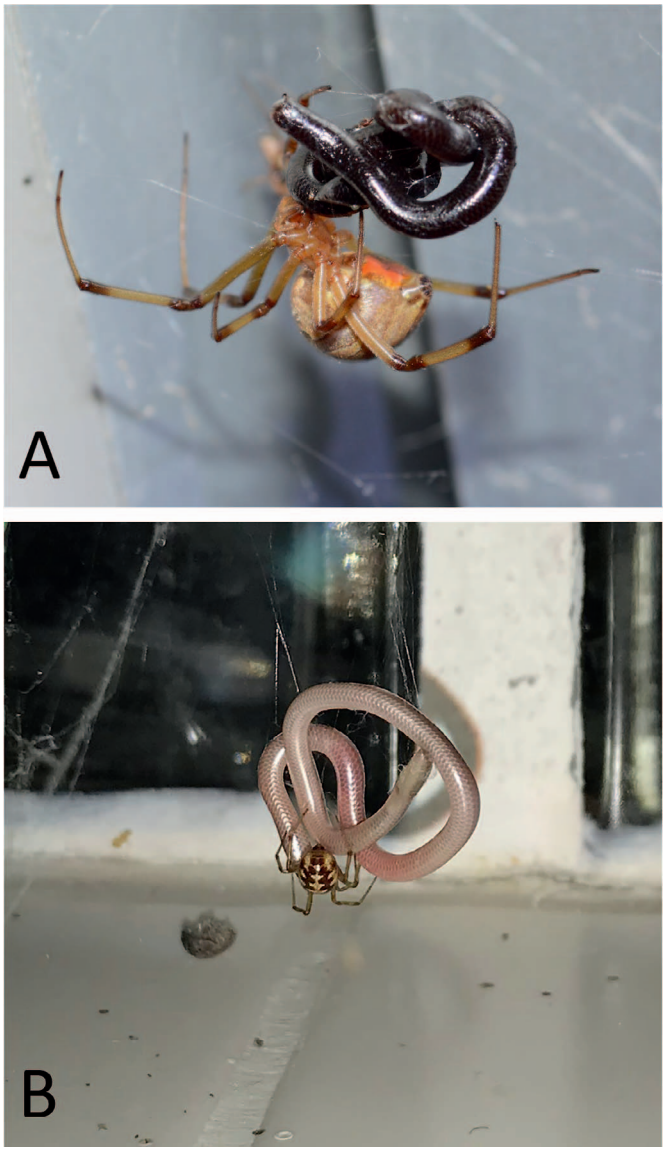

Figure 1.—Blind snakes killed in webs of theridiid spiders. A. Brown widow spider, *Latrodectus geometricus*, feeding on a Brahminy blindsnake, *Indotyphlops braminus* (Typhlopidae), in a garden house in Zaachila, Oaxaca, Mexico (Photo by Matias Martinez). B. Texas Blind Snake, *Rena dulcis* (Leptotyphlopidae), trapped in web of the theridiid spider *Steatoda triangulosa* in a building near San Antonio, Texas, USA (Photo by George Popescu).

nosed snakes (*Heterodon platirhinos*), king snakes (*Lampropeltis calligaster* and *Lampropeltis triangulum*), lined snakes (*Tropidoclonion lineatum*), night snakes (*Hypsiglena chlorophaea*), racers (*Coluber constrictor*), rat snakes (*Pantherophis guttatus*), ringneck snakes (*Diadophis punctatus*), sand snakes (*Sonora straminea*), scarlet snakes (*Cemophora coccinea*), and watersnakes (*Nerodia sipedon* and *Nerodia rhombifer*) (Appendix 2). Among these North American colubrids, ringneck snakes and garter snakes have been reported to be trapped in spider webs particularly frequently (e.g., Burt 1949; Groves & Groves 1978; Klemens 1993).

That Elapidae are the snake group second most frequently killed by spiders can be explained by the numerical predominance of this snake family in Australia (Shine 1977). Brown snakes (*Pseudonaja* spp.) are particularly frequently killed by Australian spiders (Fig. 5A; also see De Rebeira 1981; Bush 1989; Peters 2016; Australian Museum 2020).

3.3 Global distribution of snake predation by spiders.—Predation on snakes by spiders has been witnessed so far in 25 countries (see Supplementary Table S1). Predation on snakes by spiders is a global pattern occurring on all continents except Antarctica. The vast majority of reports of snake predation by spiders originates from the USA (51% of all naturally occurring incidents) and Australia (29%). In USA, snake predation by spiders is known from 29 states and all parts of the country except Alaska (Supplementary Table S1).

To a lower extent, incidents of snake predation were reported from the Neotropics (8%), Asia (6%), Africa (3%), Canada (1%), and Europe (<1%). The two European reports both refer to incidents of predation upon tiny blind snakes (*Indotyphlops braminus* and *Xerotyphlops vermicularis*: Petrov & Lazarov 2000; Faraone et al. 2019), whereas the Canadian reports deal with neonate ringneck snakes (*Diadophis punctatus*) and presumably a juvenile wandering gartersnake (*Thamnophis elegans*) trapped in spider webs (The Spider Club of SA 2018; Algonquin Wildlife Research Station 2020; Malgonquin Photography 2020).

3.4 How spiders kill snakes.—Eighty-seven percent of the snakes captured by spiders got killed, 1.5% could escape on their own, and 11% were rescued by humans (see Supplementary Table S1). The different groups of snake-eating spiders employ different methods to capture and kill their prey. In the following, we explain the killing behavior of the three dominant groups of ophiophagous spiders (black widows, tarantulas, and large orb-weavers).

Black widows build an irregular tangle of threads at a height of ≈10–100 cm above the substrate. From there, vertical sticky gumfooted threads extend to the substrate (Blackledge et al. 2005; Blackledge & Zevenbergen 2007). The webs are very strong and tough, enabling the spiders to capture prey many times larger and heavier than themselves (see Shao & Vollrath 1999; Blackledge et al. 2005; Swanson et al. 2006; Nyffeler & Vetter 2018). When a small snake slides into such a web, it sticks to the vertical viscid threads. The spider approaches the snake, throws sticky silk masses over it, and bites it one or more times (Vollrath 2000). The neurotoxin thereby injected is a very potent, vertebrate-specific toxin (α-latrotoxin) that has proven to be highly lethal to small vertebrates (Gendreau et al. 2017; Nyffeler & Vetter 2018). Subsequently the spider pulls its victim off the ground, raising it between 10 and 120 cm above the floor, a process which may last several hours (Figs. 1A, 2B, 3–5; Anonymous 1932a; Ervin & Carroll 2007; Jones et al. 2011; Stevenson & Crook 2018).

The time it took a theridiid to kill a snake varied greatly. In some instances, the snake was paralyzed a few minutes after the venomous bite had been administered by the spider (e.g., Krumm-Heller 1910). In other instances, it took a spider several days to kill a snake (Gudger 1925; Anonymous 1932b; Anonymous 1946). Unfortunately, in quite a number of reports of theridiid predation upon snakes, the spiders remained unidentified. Nevertheless, based on the specific behavior of lifting the snake off the ground, it can be assumed that in such cases the spiders in question must have been

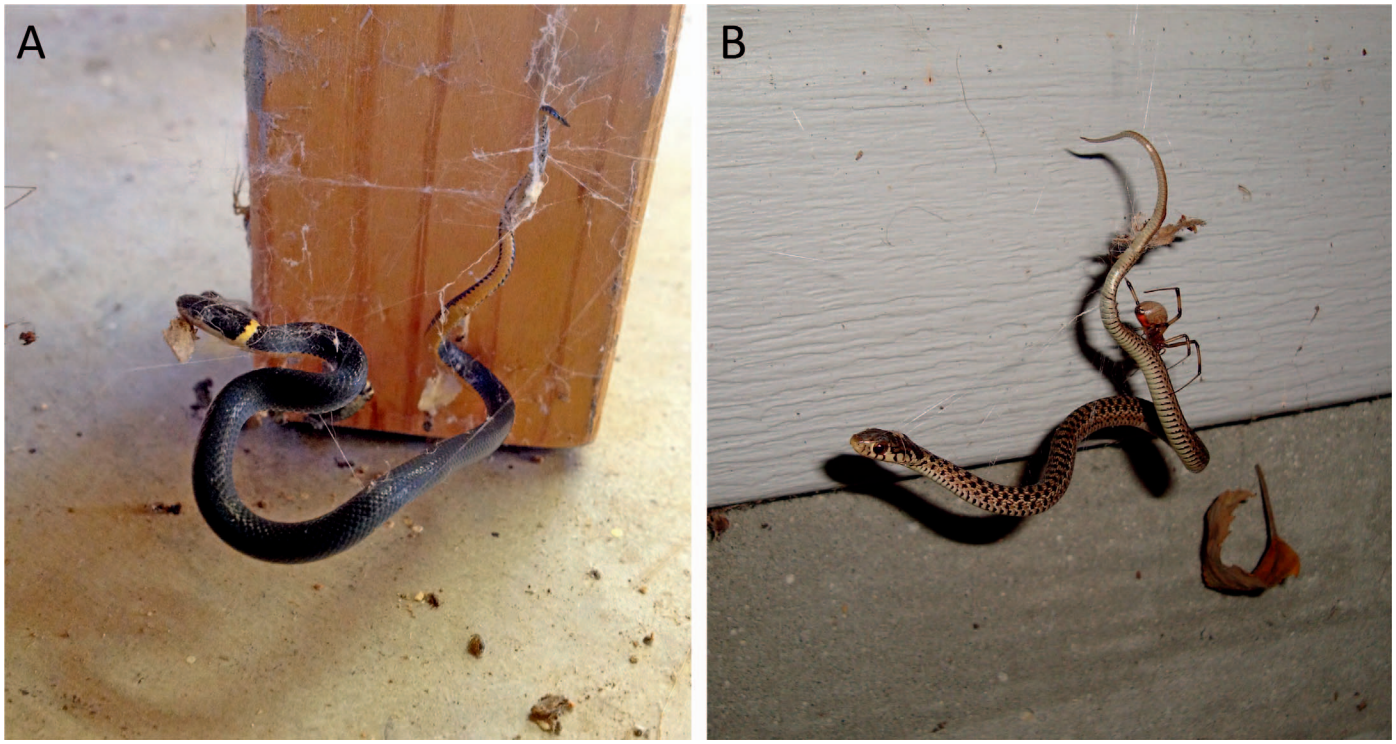

Figure 2.—Theridiid spiders capturing colubrid snakes. A. Southern Ringneck Snake, *Diadophis punctatus punctatus* (Colubridae), caught in a spider web in a garage in Virginia, USA (Photo by Erika Packard). The spider in question was a non-widow theridiid (most likely *Parasteatoda tepidariorum* (C. L. Koch, 1841)). B. Juvenile Eastern garter snake, *Thamnophis sirtalis*, trapped in a brown widow web (*Latrodectus geometricus*) observed in Douglas, Georgia, USA (Photo by Julia Safer).

Figure 3.—Black widow spiders killing colubrid snakes. A. Lined snake, *Tropidoclonion lineatum* (Colubridae), killed in web of black widow spider (*Latrodectus* sp.) in a building in Tulsa, Oklahoma, USA (Photo by Jeff Lewis). B. Juvenile scarlet snake (*Cemophora coccinea*, Colubridae) entrapped on web of *Latrodectus geometricus*, observed in a private residence in Georgia, USA (Photo by Daniel R. Crook).

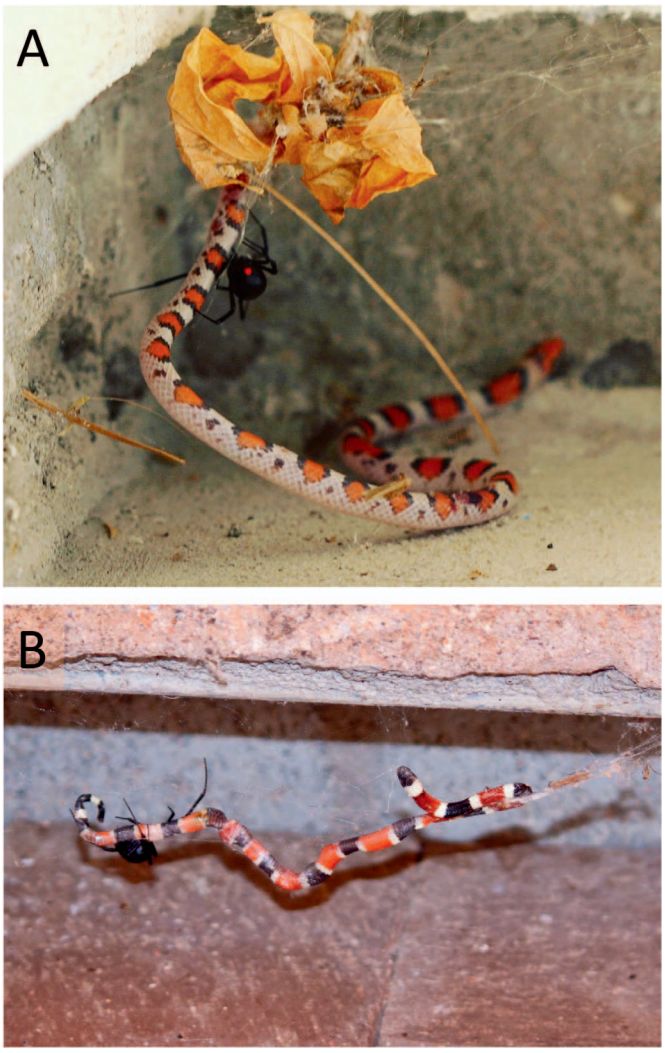

Figure 4.—Black widow spiders killing snakes. A. Scarlet snake (*Cemophora coccinea*) entrapped and killed in a black widow web (*Latrodectus* sp.) in the corner of the front porch of a house in Gulf Breeze, Florida, USA (Photo by Trisha Haas). B. Adult female black widow (*Latrodectus hesperus*) feeding on a subadult coral snake *Micruroides euryxanthus* (Elapidae) near the Boyce Thompson Arboretum, Superior, Arizona, USA (Photo by Lawrence L. C. Jones).

theridiids (see Nyffeler & Vetter 2018); but it remained open whether the predator in question was a species in the genus *Latrodectus* Walckenaer, 1805, *Parasteatoda* Archer, 1946 or *Steatoda* Sundevall, 1833. Reports according to which snakes were killed fairly rapidly seem to refer exclusively to widow spiders (*Latrodectus* spp.) (Krumm-Heller 1910; Bush 1961; Sweeney 2009; Anonymous 2016). This makes sense when taking into account that the very potent α-latrotoxin present in the *Latrodectus* venom is expected to reduce the time it takes to kill a snake. On the contrary, it seems likely that several instances in which it took a long time to kill a snake can be attributed to non-widow theridiids (e.g., *Parasteatoda* or *Steatoda*) which lack the potent α-latrotoxin in their venom and which produce a lower quantity of toxin due to their smaller body size (≈0.02–0.07 g) compared to the *Latrodectus*

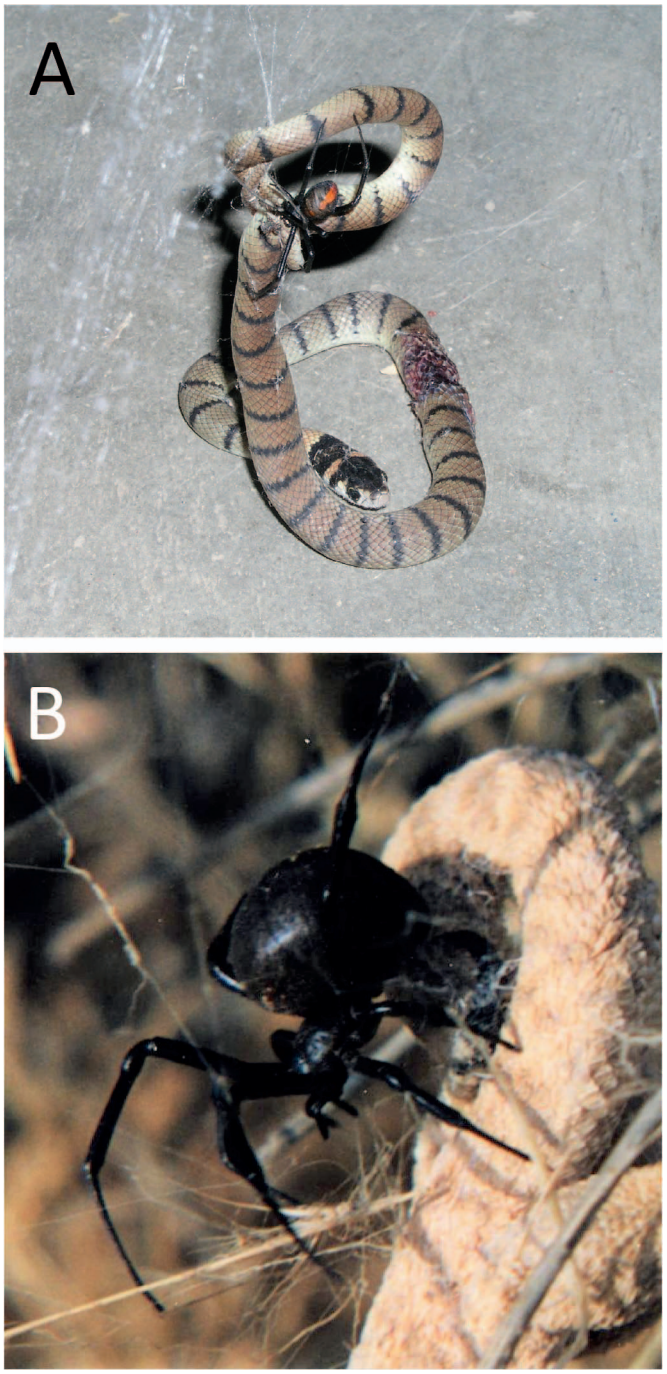

Figure 5.—Black widow spiders killing snakes. A. Juvenile Eastern brown snake, *Pseudonaja textilis* (Elapidae), killed by a redback spider (*Latrodectus hasselti*) in Australia (Photo provided by the Australian Museum, © Kevin Moore). B. Widow spider, *Latrodectus revivensis*, was feeding for several days on a dead sand viper *Cerastes vipera* (Viperidae) in the Negev desert (Photo by Ori Segev).

spp.. However, instances in which it took widow spiders several hours to kill a snake have been reported as well (e.g., De Rebeira 1981).

Tarantulas are equipped with powerful orthognath chelicerae and produce neurotoxins effectively targeting the snake nervous system (Figs. 6, 7A; Emerton 1926; Borges et al. 2016;

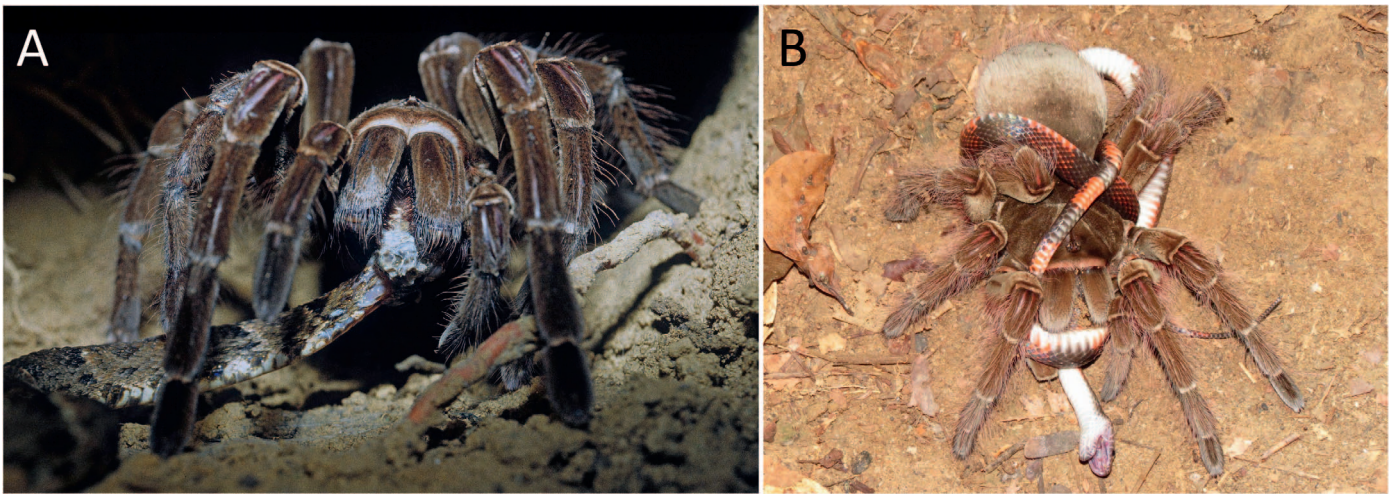

Figure 6.—Tarantulas killing and eating snakes. A. Fer-de-lance, *Bothrops atrox*, captured, killed and consumed by a *Theraphosa blondi* in Venezuela (staged incident photographed by Rick West). B. *Theraphosa blondi* capturing a juvenile false coralsnake, *Oxyrhopus* sp. (Colubridae), ≈30 cm in length, on forest floor at Senador José Porfírio municipality, Pará state, Brazil. Subsequently, the spider transported the snake to its burrow (Photo by Karll Cavalcante Pinto).

Almeida et al. 2019). Based on laboratory feeding trials, the toxicologists Brazil & Vellard investigated the snake-catching behavior of *Grammostola actaeon* (Pocock, 1903), a large Brazilian tarantula (Emerton 1926). Emerton (1926) summarizes their observations as follows: "….the spider tries to catch the snake by the head and will hold on in spite of all efforts of the snake to shake him off. After a minute or two the spider's poison takes effect, and the snake becomes quiet. Beginning at the head, the spider crushes the snake with its chelicerae and feeds upon its soft parts, sometimes taking 24 hours or more to suck the whole animal, leaving the remains in a shapeless mass…." *Theraphosa blondi* (Latreille, 1804), another huge Neotropical tarantula, was seen feeding on a snake prey for 18 hours (Rick West, pers. comm.).

Tree snakes and other colubrids occasionally get trapped in the sticky webs of large araneid and nephilid orb-weaving

Figure 7.—Nonweb-building spiders killing and eating snakes. A. Adult male tarantula (*Brachypelma* sp.) preying on a juvenile fer-de-lance, *Bothrops asper* (Viperidae), in the Yaxchilan Archaeological Zone, Chiapas, Mexico (Photo by Silvano Lopez & Danniella Sherwood; © Silvano Lopez). B. Fishing spider *Dolomedes tenebrosus* Hentz, 1844 preying on a Middle American burrowing snake, *Adelphicos quadrivirgatum* (Colubridae), in the La Estanzuela Natural Park, Nuevo Leon State, Mexico (Photo by Salvador Contreras-Arquieta).

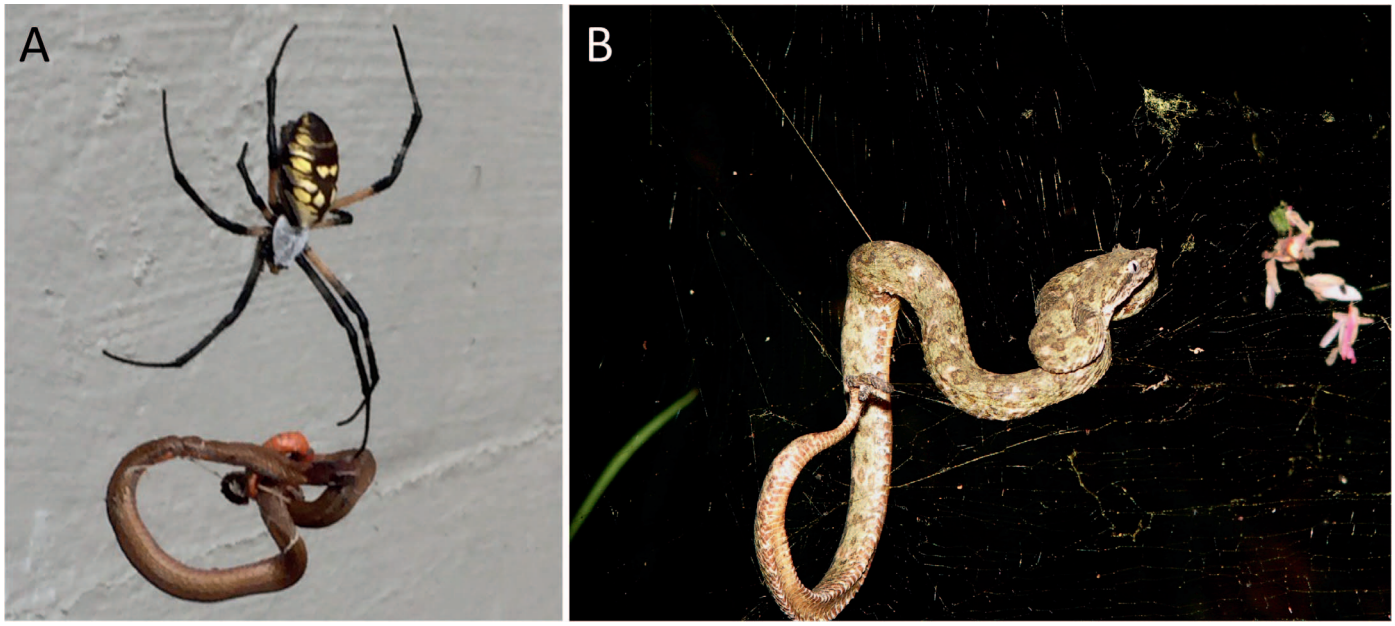

Figure 8.—Snakes killed by large orb-weaving spiders. A. *Argiope aurantia* Lucas, 1833 eats red-bellied snake, *Storeria occipitomaculata* (Colubridae), in North Carolina (Photo by Eleanor Spicer Rice). B. Eyelash Viper *Bothriechis schlegelii* (Viperidae), ≈40 cm in length, has been captured in web of *Trichonephila clavipes* (Nephilidae) in Costa Rica rain forest (Photo by Jonathan Sequeira).

spiders (genera *Argiope*, *Nephila*, and *Trichonephila*) while moving across vegetation. Once a snake is entangled in a web, the spider wraps it tightly in silk, followed by one or more venomous bites (Fig. 8A; Anonymous 1911; Pinkus 1932). After the snake's death, the spider extracts the dissolved tissue from its victim by the process of extraintestinal digestion.

3.5 Clash of the venomous: black widow spiders vs. venomous snakes.—About half of all spiders engaged in snake predation belong to spider taxa that produce neurotoxins of high toxicity. Included among these highly toxic spider species are at least seven species of widows (*Latrodectus* spp.; Figs. 1A, 2B, 3–5) in addition to wandering spiders (*Phoneutria* sp.), whereas the neurotoxins of most theraphosids are somewhat less toxic and usually harmless to humans (Foelix 2011).

By comparison, ≈30% of all snakes captured by spiders belong to species known as venomous snakes (according to the definition presented in the Methods section). Among those, a large number of species are considered highly toxic, such as New World coral snakes, Australian brown snakes (*Pseudonaja* spp.), rattlesnakes (*Crotalus* spp.), and Neotropical lanceheads (*Bothrops* spp.)(Figs. 4B, 5, 6A, 7A, 8B). One Australian species killed by spiders – the Eastern brown snake *Pseudonaja textilis* – is even considered to be one of the world's most toxic snakes to humans (Hoy 2012; Fig. 5A).

Toxicity values (expressed as LD_{50} in mice) of venomous snakes and spiders are compared in Table 4. It follows that the LD_{50} values of venomous spiders do not differ statistically significantly from those of venomous snakes (Mann-Whitney U test, $n_1 = 13$ [for spiders], $n_2 = 16$ [for snakes], $Z = 0.3947$, $P > 0.05$). In other words, spiders equipped with very potent venoms are at times attacking, killing, and consuming some highly lethal snakes, whereby the high toxicity of these snakes has so far only been proven in primates, some other mammals, birds, fish, lizards, and snakes. We know of no documented record in which a venomous snake captured by a spider has envenomated the spider. Thus, we don't know whether spiders might be vulnerable or immune to snake venoms. We know, however, that the venomous snakes from the families Elapidae and Viperidae (Table 4) feed more or less exclusively on vertebrate prey (e.g., Mao 1970; Klauber 1997; Goodyear & Pianka 2008). This indicates that it is less likely that spiders are vulnerable to snake venom because there was no need for this type of snake to evolve a specific toxin aimed to target the spider nervous system to facilitate the capture of spider prey. In spite of that, a snake bite could become lethal to a spider if the snake would succeed to puncture the spider's body with its fangs (Rick Vetter, pers. comm.).

Apart from feeding on venomous snakes, spiders at times also feed on poisonous snakes (i.e., snakes which became poisonous after feeding on toxic prey). As pointed out in the Methods section, the common garter snake (*Thamnophis sirtalis*) can be poisonous to a natural enemy after being consumed by it (Williams et al. 2004). The common garter snake is among the snakes most frequently captured by spiders in USA (Fig. 2B; Supplementary Table S1). But as far as known to us, spiders which consumed garter snakes survived such incidents without apparent harm.

3.6 Predator-prey size ratio.—Black widow spiders can overcome snakes 15–30 times their own size (Sutton 2016; Rocha et al. 2017; Fig. 12). For comparison, it is known that black widows can overcome mice of up to 14.4 times the spider's body mass (Nyffeler & Vetter 2018). An even more extreme example was reported in 1933 in the National Geographic Magazine (Anonymous 1933). In this particular case, a 15 cm long garter snake (weighing 8 g) was found trapped in the web of a triangulate cobweb spider, *Steatoda triangulosa* (Walckenaer, 1802), of only 0.0225 g body mass. Hence, this snake was 355 times heavier than the spider.

Table 2.—Total lengths and body weights of selected snake species based on literature data.

Snake species	Stage	Total length (cm)	Body mass (g)	Reference
Colubridae				
Adelphicos newmanorum	N/A	32*	8.4	Rojas-González & Zamora-Abrego 2016
Boiga irregularis	Neonate	45*	11	Mathies & Miller 2003
Coluber constrictor	Neonate	30	6.3	https://www.virginiaherpetologicalsociety.com/
Contia tenuis	Neonate	11	0.8	Leonard et al. 1996; Govindarajulu et al. 2011
Dendrelaphis pictus	Neonate	13–32	2.1–5.6	Yudhana et al. 2019
Diadophis punctatus	Neonate	11–16	0.6–1.1	https://www.virginiaherpetologicalsociety.com/
Heterodon platirhinos	Neonate	17–25	5.3	https://www.virginiaherpetologicalsociety.com/; Palmer & Braswell 1995
Lampropeltis triangulum	Neonate	20–23	4.1	https://www.virginiaherpetologicalsociety.com/
Nerodia sipedon	Neonate	19.5–25.5	3.5	Palmer & Braswell 1995
Pantherophis guttatus	Neonate	23–33	8	https://www.virginiaherpetologicalsociety.com/
Opheodrys aestivus	Adult female	$\leq$ 100	$\leq$ 45	https://www.virginiaherpetologicalsociety.com/
Opheodrys aestivus	Neonate	10.5–24.5	1.4–2.0	https://www.virginiaherpetologicalsociety.com/
Opheodrys vernalis	Neonate	13	1.1	https://www.virginiaherpetologicalsociety.com/
Oxyrhopus sp.	N/A	56	37	Crnobrna et al. 2017
Oxyrhopus sp.	Juvenile	30	6	Crnobrna et al. 2017
Storeria dekayi	Neonate	9.1	0.3	https://www.virginiaherpetologicalsociety.com/
Thamnophis sirtalis	Neonate	16–19	1.35	Palmer & Braswell 1995
Tropidoclonion lineatum	Neonate	10–11	0.45–1	Funk & Tucker 1978
Elapidae				
Hemiaspis signata	Juvenile	N/A	16	http://www.reptilerescue.com.au/short-tails/marsh-snake/ no longer available on 25 January 2021
Micruroides euryxanthus	Neonate	19–20	1.5	Lowe et al. 1986
Micrurus tener	Neonate	18–20	N/A	Quinn 1979
Pseudonaja affinis	Neonate	25.5*	4.7–6.8	Maryan & Bush 1996
Pseudonaja nuchalis	Neonate	25*	4.5–5.4	Bush 1994; https://www.qm.qld.gov.au/Find+out+about/Animals+of+Queensland/Reptiles/Snakes/Common+and+dangerous+species/Western+Brown+Snake#.Xs5NabmP6Uk
Pseudonaja textilis	Neonate	27*	3.5–10.4	https://australianmuseum.net.au/learn/animals/reptiles/eastern-brown-snake/
Lamprophiidae				
Boaedon fuliginosus	Neonate	23	4.5	Boback et al. 2012.
Typhlopidae				
Indotyphlops braminus	Juvenile	5.8	0.23	https://indiabiodiversity.org/species/show/278705
Indotyphlops braminus	Adult	6.3–16.5	0.74	https://indiabiodiversity.org/species/show/278705; https://www.floridamuseum.ufl.edu/herpetology/fl-snakes/list/indotyphlops-braminus/
Viperidae				
Bothriechis schlegelii	Subadult female	42	19	Lindey & Sorrell 2004
Bothrops asper	N/A	49	29	Henao-Duque & Ceballos 2013
Bothrops asper	Neonate	27–35	6–20	Solórzano & Cerdas 1989; Savage 2002
Bothrops jararaca	Neonate	28–32*	6–9	Furtado et al. 2006
Crotalus atrox	Neonate	20.5–37	11–25	Ernst & Ernst 2011
Crotalus durissus	Neonate	35	23	Furtado et al. 2003
Crotalus durissus	?	45	40	Klauber 1997
Sistrurus miliarius	Neonate	15–21	1.8–5.5	DeFrancesco 1987; Palmer & Braswell 1995; https://animaldiversity.org/accounts/Sistrurus_miliarius/
Trimeresurus gracilis	Adult	50	64	Lin & Tu 2008

* Roughly estimated by converting snout-vent length data to total length

Based on our survey, the largest snakes caught by spiders under natural conditions were those that became entangled in webs of *Nephila pilipes* (Fabricius, 1793) and *Trichonephila clavipes*. These are spiders with a weight of ≈1–7 g that spin orb-webs with a diameter of 0.5–1.5 m (Nyffeler & Knörnschild 2013). Snakes of ≈40–100 cm total length are captured in the strong webs of *Trichonephila clavipes* (Zippel & Kirkland 1998; Sequeira 2011), which would correspond to an estimated maximum snake weight of ≈10–45 g (Table 2). Spiders in the genera *Nephila* and *Trichonephila* have previously been reported trapping birds and bats many times heavier than themselves in their exceedingly strong webs (Brooks 2012; Nyffeler & Knörnschild 2013). In Taiwan, a Kikuchi Habu, *Trimeresurus gracilis* (Viperidae), weighing an estimated ≈60 g (Table 2), became entangled in a *Nephila pilipes* web. After the snake was fighting for its life for many hours, the web finally broke and the snake fell to the floor in a near dead state (Shanghaiist 2014). Another interesting

Table 3.—Snake families reported to be victims of spider predation (based on 319 incidents reported in the scientific literature or social media).

Taxon #	Snake family	Number of species within family	Number of predation events	Source
01	Colubridae	50	162	Neill 1948; Owens 1949; Myers 1974; Groves & Groves 1978; Klemens 1993; Zippel & Kirkland 1998; Punzo & Henderson 1999; Tanaka & Mori 2000; National Geographic Magazine 2001; Linzey & Clifford 2002; Lazcano et al. 2005; Gerald 2006; De Sousa et al. 2007; Ervin & Carroll 2007; Hall & Johnson 2007; Pruett & Jadin 2010; Aguilar-López et al. 2014; Pinto et al. 2017; Rocha et al. 2017; Sorokin & Stuckert 2017; Stevenson & Crook 2018; Da Silva et al. 2019; and others
02	Dipsadidae	2	2	Borges et al. 2016; and others
03	Elapidae	17	76	McKeown 1943; De Rebeira 1981; Bush 1989: Orange 1990; Nunes 2010; Jones et al. 2011; Peters 2016; and others
04	Lamprophiidae	5	10	Newlands 1978; Bayliss 2001; Beaman & Tucker 2014; and others
05	Leptotyphlopidae	3	8	Klauber 1940; Loomis & Stephens 1967; Branch 1998
06	Typhlopidae	2	9	Petrov & Lazarov 2000; Martínez-Coronel & Navarrete-Jiménez 2018; Faraone et al. 2019; Leets-Rodríguez et al. 2019; and others
07	Viperidae	11	17	Krumm-Heller 1910; Bush 1961; Punzo & Henderson 1999; Avila & Porfirio 2008; Sasa et al. 2009; Almeida et al. 2019; Lubin & Segev, pers. comm.; and others
—	Unspecified	N/A	35	Wilder 1865; Brown 1895; Baerg 1938; Sanders 1982; Main 1996; Durigo 2010; and others
Total		91	319	

incident was witnessed in India. There, after a bronzeback tree snake (*Dendrelaphis* sp.) of almost 100 cm total length got temporarily entangled in a *Nephila pilipes* web, the spider intentionally broke off some of the capture threads, thereby enabling the snake to escape from the web (Ashwini Kumar Bhat, pers. comm., online at http://sumasuta.blogspot.com/2008/09/tale-of-hanging-unfortunate.html).

Not only giant orb-weaving spiders, but also large tarantulas are capable of killing larger snakes. Tarantulas have been reported killing snakes of 25–56 cm total length (Gudger 1931; Borges et al. 2016; Pinto et al. 2017; Almeida et al. 2019; Rick West, pers. comm.). The largest tarantula species are those in the genera *Grammostola* Simon, 1892, *Lasiodora* C. L. Koch, 1850, and *Theraphosa* Thorell, 1870 occurring in South America. Such spiders reach body weights of $\geq$ 50 g and have been observed killing pit vipers with a total length of 30–53 cm, which corresponds to a prey weight of 9–40 g (Table 2).

A comparison between USA and Australia shows that the snakes captured by Australian spiders were, on average, larger (mean = 26.9 ± 0.8 cm; median = 27.0 cm; range = 14–50 cm) compared to those captured by North American spiders (mean = 21.5 ± 2.4 cm; median = 17.9 cm; range = 6.5–100 cm). The difference is statistically significant (Mann-Whitney *U* test, $n_1 = 38$, $n_2 = 41$, $Z = 4.0622$, $P < 0.0001$). This difference might be explained by the fact that predominantly small, lightweight colubrids such as ringneck snakes (*Diadophis punctatus*), garter snakes (*Thamnophis* spp.), Dekay's brownsnake (*Storeria dekayi*), green snakes (*Opheodrys* spp.), etc., with a neonate weight of 0.3–2 g are caught by U.S. spiders, whereas Australian spiders more often prey on heavier built elapids from the *Pseudonaja*-complex weighing as neonates ≈3.5–10 g (Table 2).

Based on pooled data from all over the world, snake total body length was weakly positively correlated with spider body length ($r = 0.4136$; $P < 0.01$; Fig. 12). An apparent accumulation of dots around 1.0 on the x-axis can be explained by the fact that snake-eating spiders are made up to a large extent by adult female black widows with an estimated average body length around 1 cm.

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 has been killed and eaten by the predator (Begon et al. 2005). Under natural conditions web-building spiders (i.e., theridiids, araneids, nephilids, agelenids, and pholcids) feed more or less exclusively on prey killed in their webs. Multiple YouTube videos show snakes suspended in spider webs, often fighting for extended periods of time for their life prior to their death. In addition, numerous anecdotal reports on this have been published (e.g., Jantos 2012; Anonymous 2016; Brown 2017). Most cases of this type end with the spider feeding on the dead snake.

In vagrant hunters (theraphosids, pisaurids, and ctenids) the situation is somewhat different. These are voracious, highly opportunistic feeders which feed not only on freshly killed prey, but occasionally also on carcasses of animals that had not been killed by themselves ("scavenging": Schmidt 1957; Nyffeler & Altig 2020). Notwithstanding this, many well documented cases of predation on snakes by vagrant hunters observed in the field and in captivity have been reported in the literature (e.g., Rick West, pers. comm.; Emerton 1926; Pinto et al. 2017).

A very special case of scavenging has been observed in Singapore. There, a tiny, red colored theridiid kleptoparasite (possibly genus *Argyrodes*) was observed feeding on tissue of a

Table 4.—Toxicity of spider and snake venoms injected in mice (LD_{50} values based on literature). Route of injection: IM = intramuscular injections; IP = intraperitoneal injection; IV = intravenous injection; SI = subcutaneous injection. Low LD_{50} values indicate high toxicity. Available online at http://snakedatabase.org/pages/ld50.php Accessed 5 June 2020.

Spider / snake species	LD_{50} (mg/kg)	Injection method	Source
SPIDERS			
Theridiidae:			
Latrodectus geometricus	0.22	IM	Reyes-Lugo et al. 2009
Latrodectus hasselti	0.43–0.50	IV	Matsumura et al. 2018
Latrodectus hesperus	0.64	IP	Daly et al. 2001
Latrodectus indistinctus	0.08	IP	Muller et al. 1989
Latrodectus mactans	0.26	IP	Daly et al. 2001
Latrodectus tredecimguttatus	0.90	IV	Maretic 1987
Latrodectus variolus	1.80	N/A	McCrone 1964
Ctenidae:			
Phoneutria nigriventer	0.34	IV	Maretic 1987
Theraphosidae:			
Acanthoscurria musculosa	7.50	IV	Maretic 1967
Aphonopelma sp.	14.14	N/A	Stahnke & Johnson 1967
Pterinochilus sp.	9.00	IV	Maretic 1967
Cyriopagopus hainanus	0.20	IP	Liu et al. 2003
Theraphosa blondi	1.80	N/A	Fontana et al. 2002
Median	0.64		
SNAKES			
Elapidae:			
Micruroides euryxanthus	N/A	N/A	N/A
Micrurus ibiboboca	3.35	IP	http://snakedatabase.org/pages/ld50.php
Micrurus tener	0.64	IV	http://snakedatabase.org/pages/ld50.php
Pseudechis porphyriacus	2.52	SI	Broad et al. 1979
Pseudonaja affinis	0.66	SI	Broad et al. 1979
Pseudonaja nuchalis	0.47	SI	Broad et al. 1979
Pseudonaja textilis	0.05	SI	Broad et al. 1979
Viperidae–Vipertinae:			
Causus rhombeatus	10.28	IV	http://snakedatabase.org/pages/ld50.php
Viperidae–Crotalinae:			
Bothriechis schlegelii	1.60	IV	http://snakedatabase.org/pages/ld50.php
Bothrops asper	1.17	IV	http://snakedatabase.org/pages/ld50.php
Bothrops atrox	1.40	IV	http://snakedatabase.org/pages/ld50.php
Bothrops jararaca	0.83	IV	http://snakedatabase.org/pages/ld50.php
Bothrops moojeni	0.39	IV	http://snakedatabase.org/pages/ld50.php
Crotalus atrox	0.92	IV	http://snakedatabase.org/pages/ld50.php
Crotalus durissus	0.05	IV	http://snakedatabase.org/pages/ld50.php
Sistrurus miliarius	2.80	IV	http://snakedatabase.org/pages/ld50.php
Trimeresurus spp.	0.37–1.64	IV	http://snakedatabase.org/pages/ld50.php
Median	0.96		

painted bronzeback snake carcass which had apparently been killed in a *Nephila pilipes* web (Lim 2009).

4.2 What percentage of captured snakes was rescued by humans?—Of the captured snakes, only 11% were rescued by humans and 1.5% could escape on their own, whereas 87% were killed by spiders (see Results section). By comparison, Brooks (2012) analyzing 69 incidents of bird captures by web-building spiders found that >50% were rescued by humans, a little over 10% could escape on their own, and a little over 30% were killed by spiders. The percentages of rescued snakes vs. rescued birds differed statistically significantly (Chi-square test, $\chi^2 = 50.03$, $df = 1$, $P < 0.001$). In conclusion, the willingness to rescue a snake is lower than the willingness to free a bird. Considering that some of the snakes caught in spider webs are highly toxic to humans and that in addition to this a high percentage of the snake-catching spiders are highly toxic, it is understandable that only a small percentage of observers is willing to get involved in a snake rescue operation. This might be especially true in countries like Australia dominated by venomous elapids (e.g., brown snakes) where even a juvenile snake can administer a deadly bite to a human (Sutherland & Tibballs 2001).

4.3 Nonpredation causes by which snakes are seriously harmed by spiders.—Predation is not the only way snakes can be harmed by spiders, as the following examples demonstrate. Murphy (2014) reports tail amputation in a reticulated python (*Malayopython reticulatus*) at the Dallas Zoo due to necrosis from a brown recluse spider bite (*Loxosceles reclusa* Gertsch & Mulaik, 1940) (Sicariidae). Although no evidence of spider involvement is provided in the aforementioned case, it cannot be ruled out that the necrosis in the python was indeed caused by a recluse spider bite, since sicariid venom has been reported to produce dermonecrotic

Figure 9.—Juvenile Sonoran gopher snake (*Pituophis catenifer*) found in a building in Salem, Oregon. Its head and much of its body was wrapped up in spider webbing with other detritus (i.e., gum, small bits of paper, and pebbles) attached to it, and it is assumed that the snake either was wrapped up in spider webbing after having escaped from a spider web, or that it picked up the pocket of webbing along with the detritus while passing under a door from the building to inside. The snake's view was strongly obstructed by the amount of webbing engulfing its head indicating that its chance of survival would have been severely diminished if the bag of webbing on its head had not been removed by the human who found it in the building (Photo: Tim Akimoff).

effects on reptile tissue and reptile fatality (Ramires & Fraguas 2004; Taucare-Rios & Piel 2020).

A second case where a snake was put in danger by a nonpredation cause was witnessed in a residential area in Oregon. In that case, a juvenile Sonoran gopher snake (*Pituophis catenifer*) about 20–25 cm in length, whose head and much of its body was wrapped up in spider webbing with other detritus (i.e., gum, small bits of paper, and pebbles) attached to it, was found in a building (Tim Akimoff, pers. comm.; Fig. 9). This snake's view was strongly obstructed by the amount of webbing engulfing its head. The person who reported this incident does not believe the snake would have been able to free itself from the web. He states with regard to the webbing "….It was extremely sticky when I removed it, and I had to hold the snake's head firmly in order to get all of the webbing pulled off of it" (Tim Akimoff, pers. comm.). There are two possibilities how this snake's head got engulfed by the webbing: 1. The snake broke loose from a spider web after having gotten temporarily entangled in it; 2. The snake picked up the pocket of webbing along with the detritus while passing under a door from the building to inside (Tim Akimoff, pers. comm.). Be that as it may, due to the impaired vision this snake's chance of survival would have been severely diminished if the bag of webbing on its head had not been removed by the human who found the snake.

4.4 How important are reptiles as spider diet?—Most spiders reported in this review (i.e., Agelenidae, Araneidae, Ctenidae, Idiopidae, Lycosidae, Nephilidae, Pholcidae, Pisauridae, Sparassidae, Theraphosidae, and Theridiidae) feed to a large extent on arthropod prey, and under most circumstances snakes are probably only marginal food for them. However, there are a few exceptions to this.

In laboratory feeding experiments conducted in Brazil, the large tarantula *Grammostola actaeon* refused to eat insects offered to it (Emerton 1926). Thereafter, small snakes and frogs were offered to the spiders, and those were readily consumed (Emerton 1926). As a result of Emerton's report,

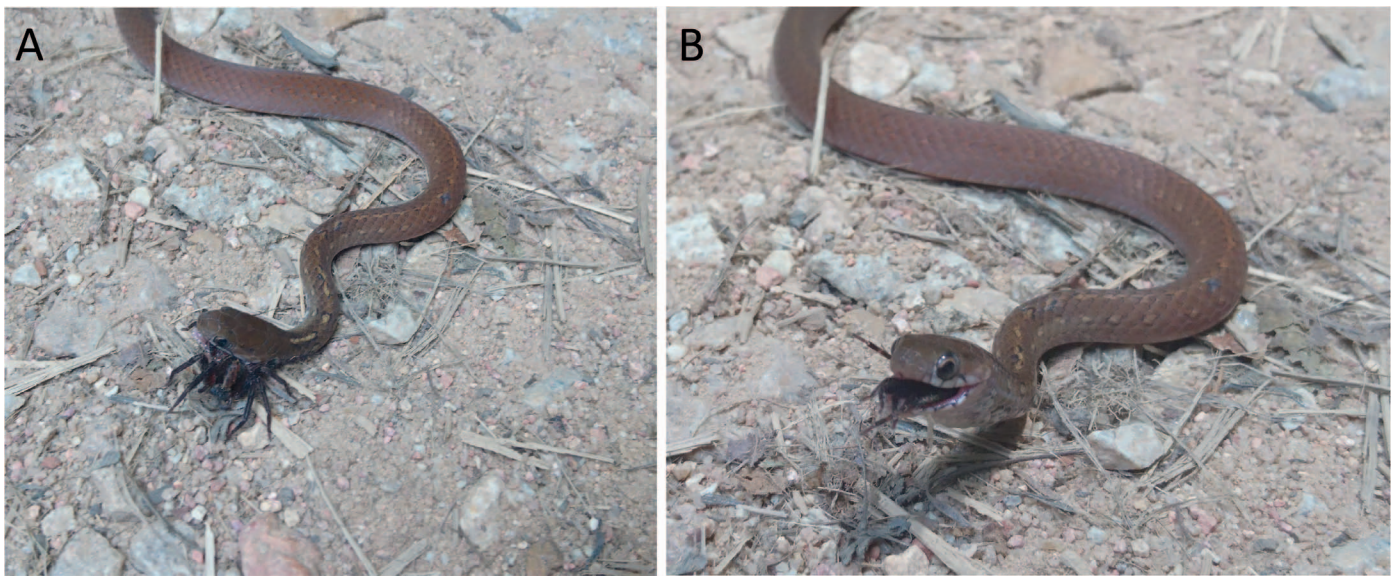

Figure 10.—A., B. Orange-bellied ringneck snake (*Gongylosoma baliodeirum*) eating a wandering spider, *Ctenus* sp., observed in the Central Catchment Nature Reserve, Singapore (Photos by Holly C. Chapman).

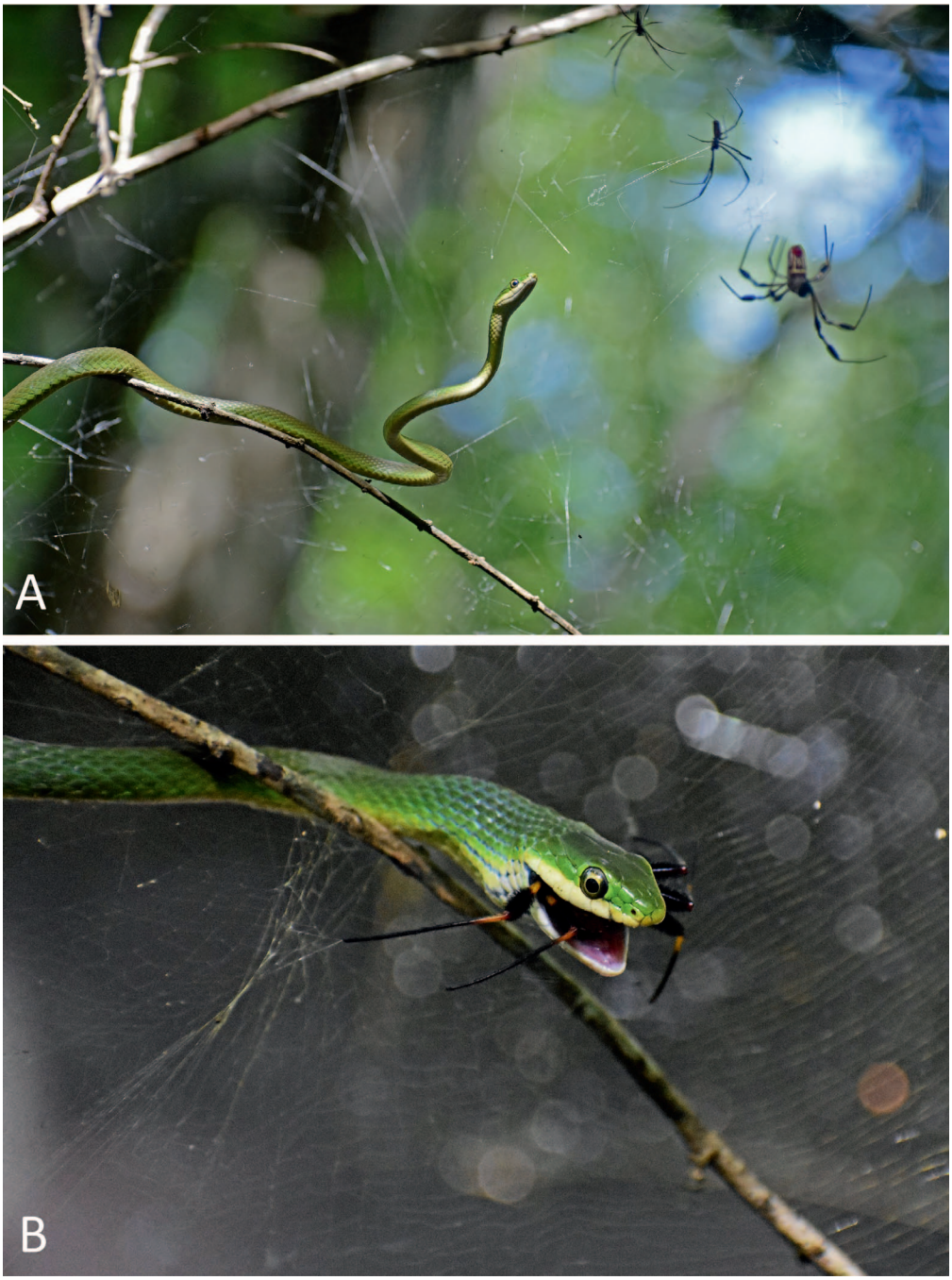

Figure 11.—Snake attack on *Trichonephila clavipes* spider photographed in West Ashley, South Carolina, USA (Photos by Max Roberts/iNaturalist CC BY-NC). A. Rough green snake, *Opheodrys aestivus* (Colubridae), approaches webs of *Trichonephila clavipes* with the attempt to catch a spider. B. Rough green snake, *Opheodrys aestivus*, has captured a *Trichonephila clavipes* spider and is swallowing it.

this tarantula species has been implied in several books to be a specialized predator of snakes and frogs (Berland 1932; Millot 1949; Gertsch 1979; Hillyard 1994). In light of newer information, the characterization of this tarantula species as a specialized snake- and frog-eater must be somewhat relativized. Contrary to Emerton's experiences, Ibler et al. (2013) were able to rear *Grammostola actaeon* on a diet of crickets, which shows that this species apparently has a broader diet than previously assumed. Apart from *Grammostola actaeon,* still other large tarantula species (e.g., *Theraphosa blondi*) kill snakes (Punzo & Henderson 1999; Aguilar-Lopez et al. 2014; Jorge et al. 2016; Pinto et al. 2017). It took large tarantulas 18–24 hours to devour snakes of 30–55 cm total length (Emerton 1926; Rick West, pers. comm.). The long feeding times reported in these cases indicate that a snake of that size is a "big, profitable meal" for a large tarantula. Tarantulas are capable of ingesting large amounts of food (thereby storing surplus energy in their body's interstitial

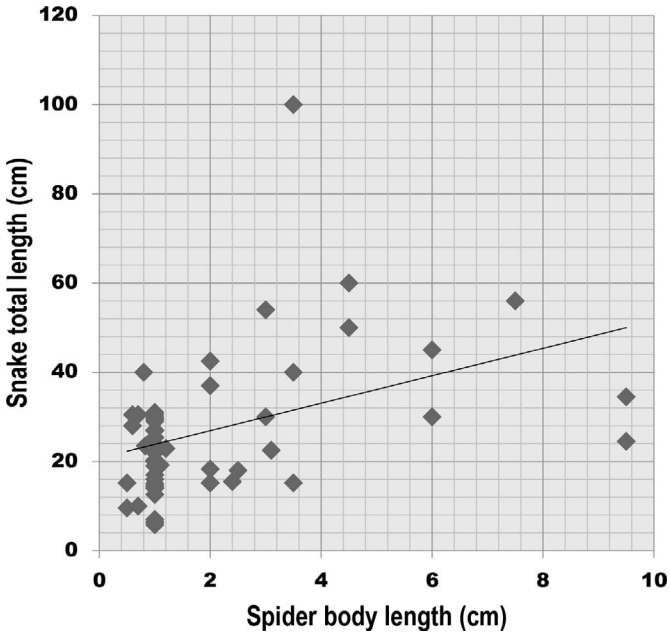

Figure 12.—Relationship between spider body length and snake body length based on 86 available data pairs. Snake body length refers to total length (snout-vent length + tail length), whereas spider body length refers to cephalothorax plus abdomen. A low positive correlation ($r = 0.4136$; $P < 0.01$) between snake body length and spider body length was found.

tissue as lipid or glycogen) and in time periods of starvation the spiders can access these stored energy reserves (Foelix 2011). Viewed this way, feeding on snakes might have long-term nutritional value, – especially in environments with irregular food availability where food can become scarce at times. Most reports of large tarantulas feeding on snakes originate from the Neotropics (Emerton 1926; Nunes et al. 2010; Aguilar-Lopez et al. 2014; Jorge et al. 2016; Pinto et al. 2017).

Not only for large tarantulas, but also for smaller sized web-building spiders, a snake prey might be a big catch. After a neonate red-bellied snake (*Storeria occipitomaculata*) fell prey to an unspecified, small web-building spider in a building in Pennsylvania, USA, the spider ate at the snake carcass for several days (Swanson 1952). A similar account was reported by Yael Lubin from the Negev desert, where a widow spider, *Latrodectus revivensis*, was seen feeding on a dead sand viper (*Cerastes vipera*) for several days (Yael Lubin & Ori Segev, pers. comm.).

The most compelling example of spiders feasting on snake prey has been reported from Western Australia. In a shed in Dongara, a scene was filmed where dozens of neonate brown snakes (Elapidae) were trapped and killed in the webs of a colony of redback spiders, *Latrodectus hasselti* (Peters 2016). This episode of redback spiders feeding heavily on reptiles does not seem to be so unusual. For instance, in a building in South Australia a redback spider had been observed catching eight lizards in succession (Poposki 2019). Altogether, a total of 27 spider families have been reported consuming reptile prey (Table 5).

4.5 Do spiders capture predominantly venomous or nonvenomous snakes?—In USA, 6 of 161 snake specimens (3.7 %) captured by spiders belong to the venomous snakes (i.e., Elapidae and Viperidae). By contrast, in Australia, 77 of 87 snakes (88.5 %) captured by spiders were venomous snakes (i.e., Elapidae, but also including the colubrid *Boiga irregularis*). This difference between the percentages is statistically highly significant (Chi-square test, $\chi^2 = 181.72$, $df = 1$; $P < 0.0001$) and can be explained by the fact that the vast majority of the snakes occurring in USA are nonvenomous colubrids (Nellis 1997), whereas the Australian snake fauna is dominated by venomous elapids (Fig. 5A; Mirtschin et al. 2002). The few North American venomous snake taxa preyed upon by spiders include coral snakes (*Micrurus*, *Micruroides*), pygmy rattlesnakes (*Sistrurus*), and rattlesnakes (*Crotalus*) (Fig. 4B; Krumm-Heller 1910; Punzo & Henderson 1999; Jones et al. 2011). The situation in the Neotropics may be somewhere in between; here 13 of 33 snake victims of spiders (39.4 %) were venomous (i.e., Elapidae and Viperidae; Figs. 6A, 7A, 8B). The percentage of venomous snakes is significantly higher in the Neotropics than in USA (Chi-square test, $\chi^2 = 39.38$, $df = 1$, $P < 0.0001$) and significantly lower than in Australia (Chi-square test, $\chi^2 = 30.50$, $df = 1$, $P < 0.0001$). The Neotropical venomous snake taxa preyed upon by spiders include coral snakes, rattlesnakes, palm-pitvipers (*Bothriechis*), and lanceheads (*Bothrops*; Emerton 1926; Avila & Porfirio 2008; Sasa et al. 2009; Nunes et al. 2010; Sequeira 2011).

4.6 How important are spiders as mortality agents of snakes?—Birds of prey, some carnivorous mammals (e.g., mongooses, opossums, and raccoons) as well as other snakes are generally considered to be the major predators of snakes (Fitch 1949; Greene 1997; Linzey & Clifford 2002; Gibbons 2017). Apart from carnivorous vertebrates, several groups of large invertebrate predators such as spiders, scorpions, praying mantises, giant water bugs, centipedes, and driver ants have been reported killing small snakes (McCormick & Polis 1982; Greene 1997; Nyffeler et al. 2017c). In their book "Snakes in question: The Smithsonian answer book" the herpetologists Zug & Ernst (2015) hypothesized that "….spiders are probably the main invertebrate predators of snakes". Similarly, Greene (1997) states in his comprehensive book on snakes "….small, tropical forest snakes may be especially vulnerable to the centipedes, spiders, and other large invertebrates common in such habitats…." Based on our review, it can be assumed that snake predation by certain spiders does indeed occur quite frequently. However, due to the fact that those spider species which are capable of killing snakes rely to a large extent on arthropods as a primary food source (Thierry Gasnier, pers. comm.; Lapinski & Tschapka 2013), spiders should be expected to play a subordinate role as mortality agents of snakes compared to the carnivorous vertebrates.

4.7 Spiders and snakes as intraguild predators.—Not only are spiders sometimes capturing and killing snakes, quite often the tables are turned – that is, a larger number of arthropod-eating snake species include spiders in their diets (Table 6; Figs. 10, 11). With few exceptions, spider-eating snakes belong to nonvenomous species in the family Colubridae (especially subfamily Colubrinae) and these snakes usually range between approx. 25 and 30 cm total length in most cases. Although

Table 5.—Spider families engaged in predation on reptiles based on literature data.

#	Spider family	Snake predation	Lizard predation	Source
01	Actinopodidae		●	https://australianmuseum.net.au/learn/animals/spiders/mouse-spiders/ Accessed 5 June 2020
02	Agelenidae	●	●	McCormick & Polis 1982; https://natornatex.wordpress.com/2015/08/25/quand-une-araignee-rencontre-un-lezard/ Accessed 5 June 2020
03	Araneidae	●	●	McCormick & Polis 1982
04	Atracidae		●	https://australianmuseum.net.au/learn/animals/spiders/sydney-funnel-web-spider/ Accessed 5 June 2020
05	Barychelidae		●	Quintero-Angel & Carr 2010
06	Ctenidae	●	●	This paper; Folt & Lapinski 2017
07	Ctenizidae		●	Phillips & Comus 2000
08	Deinopidae		●	https://www.flickr.com/photos/wikiwill/26159898400/in/album-72157618385141206/ Accessed 7 June 2020
09	Dipluridae		●	Paz 1988
10	Filistatidae		●	https://www.naturamediterraneo.com/forum/topic.asp?TOPIC_ID=218997 Accessed 7 June 2020
11	Halonoproctidae[A]		●	http://www.desertmuseum.org/books/nhsd_trapdoor_spider.php Accessed 7 June 2020
12	Idiopidae	●	●	Main 1996
13	Linyphiidae		●	Gudger 1931
14	Lycosidae	●	●	This paper; Corey 1988
15	Nephilidae	●	●	This paper; Filipiak & Lewis 2012
16	Oxyopidae?[B]		●	https://onenicebugperday.tumblr.com/post/618839803810676736/pretty-lynx-spider-found-on-my-recycling-bin-he Accessed 7 June 2020
17	Pholcidae	●	●	This paper; Ackermann 2012
18	Pisauridae	●	●	This paper; Baba et al. 2019
19	Salticidae		●	Nyffeler et al. 2017a
20	Selenopidae		●	The Spider Club of SA. 2017
21	Sicariidae		●	Ramires & Fraguas 2004; Taucare-Rios & Piel 2020
22	Sparassidae	●	●	This paper; McCormick & Polis 1982
23	Tetragnathidae		●	Chatfield et al. 2014
24	Theraphosidae	●	●	McCormick & Polis 1982
25	Theridiidae	●	●	McCormick & Polis 1982
26	Thomisidae		●	Wood 2017
27	Trechaleidae		●	Folt & Lapinski 2017

[A] *Ummidia* sp. feeding on lizards; [B] *Peucetia viridans* (Hentz, 1832) presumably killed a small lizard.

spider-eating snakes feed for the most part on small, defenseless spiders (Plummer 1981, 1991; Degenhardt et al. 2005; Marques et al. 2006), there are exceptional cases in which large and/or highly toxic spiders considered dangerous prey are swallowed by snakes (Campbell 1999; Branch 2016; Holly Chapman, pers. comm.; Max Roberts, pers. comm.). In such instances, a captured spider may try to bite its captor in the mouth which might be a risky venture for the snake (Marques et al. 2006). In the following, we will present a few examples of risky snake/spider encounters.

Two snakes endemic to Mexico and Central America – the Degenhardt's Scorpion-eating Snake (*Stenorrhina degenhardtii*) and the Blood Snake (*Stenorrhina freminvillei*) are expert arachnid hunters that feed more or less exclusively on theraphosids and scorpions (Censky & McCoy 1988; Campbell 1999; Holm 2008; Köhler et al. 2017). These snakes appear to be immune to the stings of scorpions (Alvarez del Toro 1972).

In the Sonoran Desert (North America), numerous species of small, fossorial snakes occur that feed heavily on small spiders (Babb et al. 2005; Holm 2008; Smith et al. 2008). In stomach and fecal samples of the ground snake (*Sonora semiannulata*), the remains of black widow spiders and small scorpions are commonly detected, implying that these types of venomous arachnids are habitually consumed by these snakes, apparently without harming them (Funk 1967; Degenhardt et al. 2005). Black widow spiders were fed to the western shovel nose snake (*Sonora occipitalis*) in captivity – without any negative implications for the snakes (Funk 1967).

Last but not least, we wish to mention the example of the North American green snakes, the rough green snake (*Opheodrys aestivus*), which is frequently arboreal and commonly reaches a length of 80 cm, and the smooth green snake (*Opheodrys vernalis*), a ground dwelling species, which is smaller with an adult length of ≈50 cm. These snakes are known to feed heavily on spiders (Plummer 1981, 1991; Redder et al. 2006; Baldwin 2007). The vast majority of spiders captured by the green snakes are small and defenseless; however, occasionally rough green snakes snatch large orb-weaving spiders from large orb-webs (genera *Argiope* and *Trichonephila*) (Fig. 11; Anonymous 2020; Max Roberts, pers. comm.). To approach large orb-webs with the purpose of catching their inhabitants (Fig. 11A) can be a risky endeavor for these snakes which can get entangled irreversibly in the spiders' strong sticky webs (Gudger 1931; Zippel & Kirkland 1998).

Table 6.—Examples of colubrid snake species reported to feed on spiders, with percent spiders in the snakes' total diet (based on literature data).

Scientific name	Common name	Geographic region	percent spiders in the total of prey items	Source
Colubrinae				
Coronella girondica	Southern Smooth Snake	Italy	5	Luiselli et al. 2001
Eirenis collaris	Collared Dwarf Racer	Turkmenistan	67–75	Dotsenko 1987
Eirenis medus	N/A	Turkmenistan	52	Dotsenko 2000
Eirenis modestus	Asia Minor Dwarf Racer	Turkmenistan	49–60	Dotsenko 1987
Ficimia streckeri	Mexican Hooknose Snake	Texas	High percent spiders	Werler & Dixon 2000
Gyalopion canum	Western Hooknose Snake	Sonoran desert	85	Hardy 1975; Holm 2008
Gyalopion quadrangulare	Thornscrub Hooknose Snake	Mostly USA?	31	Babb et al. 2005
Opheodrys aestivus	Rough greensnake	Arkansas	25–69	Plummer 1981, 1991
Opheodrys vernalis	Smooth Green Snake	Michigan	38	Baldwin 2007
Philodryas agassizii	Burrowing Night Snake	Brazil	72	Marques et al. 2006
Sonora aemula	Filetail Ground Snake	Mexico	20	Smith et al. 2008
Sonora fasciata	Variable Sand Snake	Sonoran desert	13	Holm 2008
Sonora occipitalis	Western Shovelnose Snake	Sonoran desert	16	Holm 2008
Sonora palarostris	Sonoran Shovelnose Snake	Sonoran desert	47	Holm 2008
Sonora semiannulata	Ground Snake	Sonoran desert	38	Holm 2008
Stenorrhina degenhardtii	Degenhardt's Scorpion-eating Snake	Central America	high percent spiders	Campbell 1999; Holm 2008
Stenorrhina freminvillei	Blood Snake	Central America, Mexico	high percent spiders	Censky & McCoy 1988; Campbell 1999; Holm 2008
Natricinae				
Natriciteres sylvatica	Forest Marsh Snake	Southern Africa	high percent spiders	Branch 2016
Insertae sedis				
Gongylosoma baliodeira	Striped Ringneck	Southeast Asia	high percent spiders	Fig. 10 (this paper); Stuebing & Inger 1999; Robert Inger, pers. comm.
Gongylosoma longicaudum	Long-tailed Ringneck	Southeast Asia	high percent spiders	Das 2015

5. CONCLUDING REMARKS

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 this enormous appetite, the spiders must acquire enough food from a broad variety of food sources (see Nyffeler & Symondson 2001; Nyffeler & Knörnschild 2013; Nyffeler & Pusey 2014; Nyffeler et al. 2016, 2017a,b; Nyffeler & Vetter 2018). To this effect, the use of vertebrates as a supplementary food source by spiders represents an opportunity to enlarge their food base, resulting in enhanced chance of survival. Interestingly the snakes captured by spiders also encompasses some species from the families Elapidae and Viperidae known to be highly toxic to humans and other vertebrates, however, there is so far no evidence in the literature that a venomous snake captured by a spider has envenomated the spider.

ACKNOWLEDGMENTS

Thanks to Robb Bennett (Royal British Columbia Museum), Ansie Dippenaar-Schoeman (University of Pretoria), G.B. Edwards (Curator Emeritus, Florida State Collection of Arthropods, Gainesville), Hubert Höfer (State Museum of Natural History, Karlsruhe), Peter Jäger (Senckenberg Research Institute, Frankfurt), Kelly Kissane (Trinidad State Junior College), Yael Lubin (Ben-Gurion University), Robert Raven (Queensland Museum), Barbara Thaler-Knoflach (University of Innsbruck), and Rick West (Sooke, British Columbia) for identifying spiders in photos. We also thank William Lamar (formerly University of Texas), Rick Shine (University of Sidney and Macquarie University), Stephen Spawls (City College Norwich), Gernot Vogel (Society for Southeast Asian Herpetology), and Romulus Whitaker (Global Snakebite Initiative, Mamallapuram, India) for identifying snakes based on photos. We are very much indebted to Yael Lubin & Ori Segev (Technion, Haifa) and to Tim Akimoff (Oregon Department of Fish and Wildlife) for providing us with unpublished information. We thank Dirk Stevenson (Altamaha Environmental Consulting, Hinesville) and Larry Jones (formerly Coronado National Forest, Supervisor's Office, Tucson) for their support. We also wish to acknowledge Jonathan Campbell (University of Texas), Ellen Censky (formerly University of Oklahoma), Holly Chapman (WWF Singapore), the late Robert Inger (Field Museum of Natural History), and Michael Plummer (Harding University) for unpublished information on spider-eating snakes. Comments of two anonymous reviewers helped improve the manuscript. Furthermore, we greatly thank the managing editor Rick Vetter (University of California at Riverside) and the editor-in-chief Deborah Smith (University of Kansas) for encouraging us to submit this paper as an invited review. Finally, we are very grateful to the Australian Museum in Sydney for photo courtesy and to all the photographers who gave permission to use their photos (see figure legends).

SUPPLEMENTARY FILE

Supplementary Table S1 - List of snake species reported captured by spiders. Online at https://doi.org/10.1636/JoA-S-20-050.s1

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Manuscript received 13 June 2020, revised 3 October 2020.

Appendix 1.—List of spider species engaged in predation (or predation attempts) on snakes. * In captivity or in staged field experiments; ** Presumably a staged event; *** Staged field experiment.

Species #	Spider species	Spider family	Type of evidence	Source
	CURSORIAL HUNTERS			
01	*Ancylometes rufus* (Walckenaer, 1837)	Ctenidae	Photo	Sorokin & Stuckert 2017
02	*Phoneutria* sp.	Ctenidae	Observation	Sasa et al. 2009
03	*Hogna carolinensis* (Walckenaer, 1805)*	Lycosidae	Video	Anonymous 2014: https://www.youtube.com/watch?v=N6ZH3oz76dw Accessed 6 June 2020
04	*Dolomedes okefinokensis* Bishop, 1924	Pisauridae	Photo	https://www.shutterstock.com/de/image-photo/spider-dolomedes-okefinokensis-eating-venomous-ringneck-519035221 Accessed 6 June 2020
05	*Dolomedes tenebrosus* Hentz, 1844	Pisauridae	Photo	Lazcano et al. 2005; Gerald 2006
06	*Dolomedes vittatus* Walckenaer, 1837	Pisauridae	Photo	https://www.youtube.com/watch?v=eashknfe7_4 Accessed 24 June 2020
07	N/A	Sparassidae	Photo/Video	https://www.recordchina.co.jp/b7342-s0-c30-d0000.html Accessed 6 June 2020; https://www.redbubble.com/people/carle/works/5493555-spider-eats-snake?p=poster Accessed 6 June 2020; https://www.youtube.com/watch?v=g3wKiVwfNxs Accessed 6 June 2020
08	*Acanthoscurria* sp.	Theraphosidae	Observation	Avila & Porfirio 2008
Same species as #08?	*Acanthoscurria geniculata* (C. L. Koch, 1841)*	Theraphosidae	Photo	Acanthoscurria geniculate eating Miami corn snake http://www.flickr.com/photos/choobaine/4075439652/ Accessed 27 March 2010 / No longer accessible on 6 June 2020
9	*Aphonopelma californicum (Ausserer, 1871)** [Nomen dubia]	Theraphosidae	Observation	Owens 1949
10	*Aphonopelma chalcodes* Chamberlin, 1940	Theraphosidae	Video	https://www.youtube.com/watch?v=N3pwdj4Uz90 Accessed 6 June 2020
11	*Aphonopelma crinitum (Pocock, 1901)**	Theraphosidae	Observation	Baerg 1938
12	*Aphonopelma hentzi* (Girard, 1852)	Theraphosidae	Observation	Punzo & Henderson 1999
13	*Brachypelma smithi* (F. O. Pickard-Cambridge, 1897)*	Theraphosidae	Video	https://www.youtube.com/watch?v=K7X6GZeDJiA Accessed 6 June 2020
14	*Avicularia* [= *Eurypelma*] sp.**	Theraphosidae	Photo	https://www.sciencephoto.com/media/85804/view/tarantula-eating-snake Accessed 6 June 2020
15	*Grammostola actaeon* (Pocock, 1903)*	Theraphosidae	Observation	Emerton 1926
16	*Grammostola (longimana) anthracina* (C. L. Koch, 1842)*	Theraphosidae	Photo	Gudger 1931
17	*Grammostola quirogai* Montes de Oca, D'Elía & Pérez-Miles, 2016	Theraphosidae	Photo	Borges et al. 2016
18	*Grammostola rosea* (Walckenaer, 1837)*	Theraphosidae	Photo	https://www.shutterstock.com/es/image-photo/rose-tarantula-eat-snake-1201892035 Accessed 6 June 2020
19	*Lasiodora parahybana* Mello-Leitão, 1917***	Theraphosidae	Video	https://www.youtube.com/watch?v=boZebIFn0P0 Accessed 6 June 2020
20	*Megaphobema velvetosoma* Schmidt, 1995*	Theraphosidae	Video	Rick West, pers. comm.
21	*Pachistopelma rufonigrum* Pocock, 1901	Theraphosidae	Photo	Nunes et al. 2010
22	*Schizopelma* sp.	Theraphosidae	Photo	Aguilar-López et al. 2014
23	*Theraphosa blondi* (Latreille, 1804)	Theraphosidae	Observation; Video	Jorge et al. 2016; Rick West, pers. comm.
24	*Theraphosa stirmi* Rudloff & Weinmann, 2010	Theraphosidae	Photo	Almeida et al. 2019
25	*Tliltocatl* sp.	Theraphosidae	Video	https://www.youtube.com/watch?v=bYUtSaMRrGo Accessed 20 May 2020 Spider ID Rick West
26	*Xenesthis immanis* (Ausserer, 1875)*	Theraphosidae	Observation	Cocroft & Hambler 1989

Appendix 1.—Continued.

Species #	Spider species	Spider family	Type of evidence	Source
	AERIAL-WEB WEAVERS			
27	*Argiope aurantia* Lucas, 1833	Araneidae	Photo	Anonymous 1911; Gudger 1931; Pinkus 1932; Burt 1949
28	*Argiope* sp. (cf. *A. flavescens* O. Pickard-Cambridge, 1880)	Araneidae	Video	https://www.youtube.com/watch?v=zqHqUvWpvdA Accessed 6 June 2020
29	*Eriophora* sp.? or *Neoscona* sp. ? (a genus different from #27-28)	Araneidae	Video	https://www.youtube.com/watch?v=jRVviYLKvPE Accessed 6 June 2020
30	*Trichonephila clavipes* (Linnaeus, 1767)	Nephilidae	Observation	Wilder 1865; Zippel & Kirkland 1998
31	*Nephila pilipes* (Fabricius, 1793)	Nephilidae	Photo	Tanaka & Mori 2000; Jantos 2012; Sarmiento & Emerson 2018
32	*Anelosimus* sp.	Theridiidae	Observation	Fritz Vollrath (pers. obs.) cited in McGuinness 2013
33	*Argyrodes* sp. (cf. *A. flavescens* O. Pickard-Cambridge, 1880)	Theridiidae	Photo	Micky Lim - https://www.flickr.com/photos/mickylim/3284721053 Accessed 6 June 2020
34	*Latrodectus geometricus* C. L. Koch, 1841	Theridiidae	Photo	Bayliss 2001; De Sousa et al. 2007; Rocha et al. 2017; Martínez-Coronel & Navarrete-Jiménez 2018; Stevenson & Crook 2018
35	*Latrodectus hasselti* Thorell, 1870	Theridiidae	Photo	De Rebeira 1981; Bush 1989; Peters 2016; and others
36	*Latrodectus hesperus* Chamberlin & Ivie, 1935	Theridiidae	Photo	Jones et al. 2011; Beaman & Tucker 2014; and others
37	*Latrodectus indistinctus* O. Pickard-Cambridge, 1904	Theridiidae	Photo	Bush 1961
38	*Latrodectus mactans* (Fabricius, 1775)	Theridiidae	Photo	Neill 1948; Stratton 2002
39	*Latrodectus revivensis* Walckenaer, 1837	Theridiidae	Photo	Yeal Lubin, pers. comm.
40	*Latrodectus variolus* Walckenaer, 1837	Theridiidae	Video	Malcolm Robertson –https://www.facebook.com/malgonquinphotography/ Accessed 6 June 2020
41	*Parasteatoda tepidariorum* (C. L. Koch, 1841)	Theridiidae	Photo	Hopkins 1878; Tanaka & Mori 2000; Davis et al. 2017
42	*Steatoda triangulosa* (Walckenaer, 1802)	Theridiidae	Photo	Petrov & Lazarov 2000; and others
Same species as #42?	*Steatoda* sp.	Theridiidae	Photo	Pruett & Jadin 2010
43	N/A	Pholcidae	Photo	https://www.dailymail.co.uk/news/article-3441686/Daddy-long-legs-spider-catches-deadly-brown-snake-web.html Accessed 6 June 2020; https://www.inaturalist.org/observations/15193547 Accessed 6 June 2020
	FUNNEL-WEB WEAVERS			
44	*Coras medicinalis* (Hentz, 1821)	Agelenidae	Observation	McCormick & Polis 1982
	TRAPDOOR-BUILDERS			
45	*Gaius villosus* Rainbow, 1914	Idiopidae	Observation	Main 1996

Appendix 2.—List of snake species reported having been captured by spiders. * Staged feeding experiment; ** Species name based on the revision of Reyes-Velasco et al. (2020).

Species #	Snake species	Snake family	Type of evidence	Source
01	*Adelphicos newmanorum*	Colubridae	Photo	Lazcano et al. 2005
02	*Arizona elegans*	Colubridae	Photo	https://i.imgur.com/2v2Sucj.jpg Accessed 8 June 2020 Snake ID William Lamar
03	*Atractus torquatus*	Colubridae	Observation	Jorge et al. 2016
04	*Boiga irregularis*	Colubridae	Photo	Jantos 2012
05	*Cemophora coccinea*	Colubridae	Photo	Stevenson & Crook 2018
06	*Chironius carinatus**	Colubridae	Video	Rick West, pers. comm.
07	*Chrysopelea paradisi*	Colubridae	Photo	Sarmiento & Emerson 2018
08	*Clelia clelia*	Colubridae	Video	https://www.youtube.com/watch?v=jRVviYLKvPE Accessed 6 June 2020
09	*Coluber constrictor*	Colubridae	Photo	Davis et al. 2017
10	*Crotaphopeltis hotamboeia*	Colubridae	Observation	Bayliss 2001
11	*Dendrelaphis pictus*	Colubridae	Photo	Micky Lim - https://www.flickr.com/photos/mickylim/3284721053 Accessed 6 June 2020 (Snake ID Gernot Vogel + Rom Whitaker)
12	*Dendrelaphis punctulatus*	Colubridae	Video	https://www.youtube.com/watch?v=0DmxPsRB680 Accessed 20 May 2020 Snake ID Rick Shine
13	*Dendrelaphis* sp. (*tristis*?)	Colubridae	Photo	Ashwini Kumar Bhat http://sumasuta.blogspot.com/2008/09/tale-of-hanging-unfortunate.html Accessed 20 May 2020 (Snake ID Gernot Vogel + Rom Whitaker)
14	*Diadophis punctatus*	Colubridae	Observation	Groves & Groves 1978; Klemens 1993; Stratton 2002
15	*Drymobius margaritiferus**	Colubridae	Photo	Tom McHugh – https://www.sciencephoto.com/media/85804/view/tarantula-eating-snake Accessed 6 June 2020
16	*Elaphe climacophora*	Colubridae	Photo	Tanaka & Mori 2000
17	*Hebius sauteri ?*	Colubridae	Photo	Dinesh Rao 2013 https://www.flickr.com/photos/dinrao/9141583949/ Accessed 20 May 2020 Snake ID Gernot Vogel
18	*Heterodon platirhinos*	Colubridae	Observation; Photo	Owens 1949; https://photobucket.com/ photo posted 27 August 2008 / not accessible on 25 January 2021; Snake ID Whit Gibbons & William Lamar
19	*Hypsiglena chlorophaea*	Colubridae	Observation	Ervin & Carroll 2007
20	*Imantodes cenchoa**	Colubridae	Video	Rick West, pers. comm.
21	*Lampropeltis calligaster*	Colubridae	Photo	http://imgur.com/JPngVbB Accessed 8 June 2020 Snake ID William Lamar
22	*Lampropeltis triangulum*	Colubridae	Observation	Hopkins 1878
23	*Leptodeira annulata*	Colubridae	Photo	Da Silva et al. 2019
24	*Lycodon rufozonatus*	Colubridae	Photo	https://www.recordchina.co.jp/b7342-s0-c30-d0000.html Accessed 20 May 2020
25	*Lycodon semicarinatus*	Colubridae	Observation	Tanaka & Mori 2000
26	*Lytorhynchus diadema*	Colubridae	Photo	http://fieldherping.eu/Forum/viewtopic.php?p=25033&sid=8b1bf064c Accessed 20 May 2020
27	*Nerodia rhombifer*	Colubridae	Video	Black widow spider caught a snake pic.twitter.com/7hrmUFKIXx — Nature is Lit (@NaturelsLit) Accessed August 21, 2020 Snake ID William Lamar
28	*Nerodia sipedon*	Colubridae	Photo	Shiner 1963 Snake ID Whit Gibbons
29	*Ninia sebae*	Colubridae	Photo	Aguilar-López et al. 2014
30	*Opheodrys aestivus*	Colubridae	Observation	Zippel & Kirkland 1998
31	*Opheodrys vernalis*	Colubridae	Photo	Neill 1948; Gibbons 2017
32	*Oxyrhopus petolarius*	Colubridae	Photo	Sorokin & Stuckert 2017
Same species as #32?	*Oxyrhopus sp.*	Colubridae	Photo	Pinto et al. 2017
33	*Pantherophis guttatus*	Colubridae	Photo	https://www.pinterest.co.uk/pin/434808539024906191/ Accessed 20 May 2020 Snake ID Whit Gibbons
34	*Pantherophis obsoletus?*	Colubridae	Video	Anonymous 1946; https://www.youtube.com/watch?v=47iigakAIN4 Accessed 6 June 2020
35	*Regina septemvittata*	Colubridae	Observation	Gerald 2006
36	*Rhadinella kinkelini*	Colubridae	Observation	Myers 1974
37	*Sonora straminea*	Colubridae	Video	https://www.youtube.com/watch?v=N3pwdj4Uz90 Accessed 20 May 2020
38	*Storeria dekayi*	Colubridae	Photo	Neill 1948; Cagle 2008

Appendix 2.—Continued.

Species #	Snake species	Snake family	Type of evidence	Source
39	*Storeria occipitomaculata*	Colubridae	Photo	Swanson 1952; Hall & Johnson 2007; Whit Gibbons, pers. comm.
40	*Tantilla coronata*	Colubridae	Observation	Telford 1966
41	*Tantilla gracilis*	Colubridae	Photo	Pruett & Jadin 2010
42	*Tantilla hobartsmithi*	Colubridae	Photo	Punzo & Henderson 1999; https://www.inaturalist.org/observations/15193547 Accessed 20 May 2020
43	*Tantilla melanocephala*	Colubridae	Photo	De Sousa et al. 2007; Rocha et al. 2017
44	*Thamnophis couchii ?*	Colubridae	Photo	http://i351.photobucket.com/albums/q448/Zetsumei001/snakeWithBlackWidow.jpg accessed 28 January 2021 Snake ID William Lamar
45	*Thamnophis cyrtopsis*	Colubridae	Photo	http://bugsinthenews.info/black-widow-spider-vs-eastern-black-necked-garter-snake-bridget-w-lake-belton-near-moffat-texas/ Accessed 20 May 2020
46	*Thamnophis elegans ?*	Colubridae	Photo	The Spider Club of SA 2018
47	*Thamnophis sirtalis*	Colubridae	Observation	Gudger 1925; Burt 1949; McCormick & Polis 1982
48	*Tropidoclonion lineatum*	Colubridae	Observation	Pinkus 1932; Davenport 1943; Moehn 1984
49	*Tropidonophis mairii ?*	Colubridae	Video	https://www.youtube.com/watch?v=zqHqUvWpvdA Accessed 20 May 2020 Snake ID Rick Shine
50	*Virginia valeriae*	Colubridae	Photo	http://imgur.com/WdmYRsN Accessed 8 June 2020 Snake ID William Lamar
51	N/A, a species different from #1-50	Colubridae	Video	https://www.youtube.com/watch?v=UJUkxyYmF_Y Accessed 20 May 2020 Snake ID Steve Spawls
52	*Coniophanes cf fissidens*	Dipsadidae	Video	https://www.youtube.com/watch?v=tPqZVuZ6gL0 Accessed 20 May 2020 Spider ID Rick West / Snake ID William Lamar
53	*Erythrolamprus almadensis*	Dipsadidae	Photo	Borges et al. 2016
54	*Cryptophis nigrescens*	Elapidae	Photo	Sweeney 2009 https://www.dailyexaminer.com.au/news/battle-of-the-fangs/4371697 Accessed 12 June 2020/ no longer available 25 January 2021.
55	*Drysdalia rhodogaster ?*	Elapidae	Photo	https://www.dailymail.co.uk/video/news/video-1163663/Snake-Vs-spider-Redback-traps-Brown-Snake-web.html Accessed 20 may 2020 Snake ID Rick Shine
56	*Furina* sp.	Elapidae	Photo	https://imgur.com/r/australia/fXEuW3l Accessed 20 May 2020 Snake ID Rick Shine
57	*Hemiaspis signata*	Elapidae	Observation	http://www.reptilerescue.com.au/short-tails/marsh-snake/ Accessed 10 April 2018 / no longer available on 20 May 2020
58	*Micruroides euryxanthus*	Elapidae	Photo	Jones et al. 2011
59	*Micrurus apiatus***	Elapidae	Video	https://www.youtube.com/watch?v=bYUtSaMRrGo Accessed 20 May 2020 Snake ID William Lamar
60	*Micrurus ibiboboca*	Elapidae	Photo	Nunes et al. 2010
61	*Micrurus tener*	Elapidae	Video	Gary Stockton - https://www.youtube.com/watch?v=eEOODYGRAyg Accessed 20 May 2020
62	*Parasuta dwyeri?*	Elapidae	Photo	Malpass 2015 The Sydney Morning Herald https://www.smh.com.au/environment/conservation/spider-v-snake-redback-spider-wins-snake-dies-from-likely-poisoning-20150303-13tgdf.html Accessed 20 May 2020 Snake ID Billy Collett, Australian Reptile Park
63	*Parasuta monachus*	Elapidae	N/A	Orange 1990
64	*Parasuta nigriceps*	Elapidae	N/A	O'Shea & Kelly 2017
65	*Pseudechis porphyriacus*	Elapidae	Photo	McKeown 1943
66	*Pseudonaja affinis*	Elapidae	Photo	De Rebeira 1981
67	*Pseudonaja nuchalis*	Elapidae	Observation	Bush 1989
68	*Pseudonaja textilis*	Elapidae	Photo	https://australianmuseum.net.au/learn/animals/insects/predators-parasites-and-parasitoids/ Photo Kevin Moore Accessed 20 May 2020
69	*Simoselaps* sp.	Elapidae	Photo	https://www.reddit.com/r/WTF/comments/2umpgn/venomous_spider_vs_venomous_snake_only_in/ Accessed 20 May 2020 Snake ID Rick Shine
70	*Suta suta*	Elapidae	Photo	https://twitter.com/dan_rabosky/status/1058141626785320963 Accessed 20 May 2020

Appendix 2.—Continued.

Species #	Snake species	Snake family	Type of evidence	Source
71	*Boaedon capensis*	Lamprophiidae	Photo	http://www.sareptiles.co.za/forum/viewtopic.php?t=7308 Accessed 20 May 2020
72	*Boaedon fuliginosus*	Lamprophiidae	Observation	Bayliss 2001
73	*Contia tenuis*	Lamprophiidae	Photo	Beaman & Tucker 2014
74	*Lamprophis aurora*	Lamprophiidae	Photo	Smith 2004 https://www.news24.com/News24/Spider-snacks-on-snake-20040211 Accessed 11 June 2020
75	*Lycophidion capense*	Lamprophiidae	Observation	Newlands 1978
76	*Leptotyphlops* sp.	Leptotyphlopidae	Observation	Branch 1998
77	*Rena dulcis*	Leptotyphlopidae	Video	https://www.youtube.com/watch?v=1XPtufzSO8A Accessed 1 March 2016 / no longer available 20 May 2020
78	*Rena humilis*	Leptotyphlopidae	Observation	Klauber 1940; Loomis & Stephens 1967
79	*Indotyphlops braminus*	Typhlopidae	Photo	Martínez-Coronel & Navarrete-Jiménez 2018; Faraone et al. 2019; Leets-Rodríguez et al. 2019
80	*Xerotyphlops vermicularis*	Typhlopidae	N/A	Petrov & Lazarov 2000
81	*Bothriechis schlegelii*	Viperidae	Photo	Jonathan Sequeira https://www.projectnoah.org/spottings/6162278 Accessed 20 May 2020
82	*Bothrops asper*	Viperidae	Observation	Sasa et al. 2009; Lopez & Sherwood 2019
83	*Bothrops atrox*	Viperidae	Photo	Almeida et al. 2019
84	*Bothrops jararaca**	Viperidae	Observation	Emerton 1926
85	*Bothrops moojeni*	Viperidae	Observation	Avila & Porfirio 2008
86	*Causus sp.*	Viperidae	Photo	Bush 1961
87	*Cerastes vipera*	Viperidae	Photo	Yael Lubin & Ori Segev, pers. comm.
89	*Crotalus atrox*	Viperidae	Observation	Punzo & Henderson 1999
88	*Crotalus durissus**	Viperidae	Photo	Emerton 1926; Gudger 1931
90	*Sistrurus miliarius*	Viperidae	Observation; Photo	Krumm-Heller 1910; https://www.reddit.com/r/natureismetal/comments/9cyrgo/pygmy_rattle snake_caught_in_a_black_widows_web/ Accessed 20 May 2020
91	*Trimeresurus gracilis*	Viperidae	Photo	http://shanghaiist.com/2014/07/05/snake-eating-spider-taiwan/ Accessed 20 May 2020 Snake ID Gernot Vogel + Rom Whitaker

Erratum

Nyffeler M, Whitfield Gibbons J. 2021. Spiders (Arachnida: Araneae) feeding on snakes (Reptilia: Squamata). *The Journal of Arachnology* 49(1):1–27.

On page 3, subsection 3.1, second paragraph we stated "….and a white colored, not uniquely identifiable Iranian widow spider (possibly *Latrodectus pallidus* O. Pickard-Cambridge, 1872)…." After the paper was published, Alireza Zamani, an expert on the spiders of Iran, informed us that the video (posted on the website of Rok News Agency Iran) was probably not produced in Iran and that the spider shown in the video is not a *Latrodectus pallidus*; instead it actually is a *Latrodectus geometricus* C. L. Koch, 1841 verified by the unique egg sacs with silk spikes on the surface which can be seen in the video as well (A. Zamani, pers. comm.).

On the other hand, according to Alireza Zamani an incident of a female comb-footed spider (*Steatoda triangulosa* (Walckenaer, 1802)) feeding upon a blind snake (Typhlopidae) – not mentioned in the Nyffeler & Gibbons (2021) paper – had been photographed in Iran (photographer: Seyed Hamze Kalantaris https://www.instagram.com/p/BxuJtTHgau_/).

In Figure 9 (page 13) the image of a colubrid snake was incorrectly identified as Sonoran gopher snake (*Pituophis catenifer* (Blainville, 1835)). According to the herpetologists Harry W. Greene, William Lamar, and Dirk Stevenson the photo most likely depicts a young racer (*Coluber constrictor* Linnaeus, 1758). This change of snake species name refers also to the text on page 13, subsection 4.3, right column, where we stated "….In that case, a juvenile Sonoran gopher snake (*Pituophis catenifer*) about 20–25 cm in length, whose head and much of its body was wrapped up in spider webbing with other detritus (i.e., gum, small bits of paper, and pebbles) attached to it, was found in a building (Tim Akimoff, pers. comm.; Fig. 9)…." This should be replaced by the sentence "….In that case, a juvenile racer (*Coluber constrictor*) about 20–25 cm in length, whose head and much of its body was wrapped up in spider webbing with other detritus (i.e., gum, small bits of paper, and pebbles) attached to it, was found in a building (Tim Akimoff, pers. comm.; Fig. 9)…."

Figure 9.—Juvenile racer (*Coluber constrictor* Linnaeus, 1758) found in a building in Salem, Oregon.

ACKNOWLEDGEMENTS

We wish to thank Alireza Zamani (University of Turku, Finland), Harry W. Greene (Cornell University, Ithaca, New York, USA), William Lamar (formerly University of Texas at Tyler, Texas, USA), and Dirk Stevenson (Altamaha Environmental Consulting, Hinesville, Georgia, USA) for pointing out these errors and correctly identifying the species in question.
https://doi.org/10.1636/JoA-S-21-300