

Chapter 9

Foraging Strategies of Cursorial and Ambush Spiders

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Abstract Food consumption in animals is a complex task with multiple steps. Choosing an adequate foraging site is the very first one, and involves not only the presence of prey and predators but also abiotic conditions. Because spiders are usually cannibalistic, conspecifics fall within these two categories in addition to being competitors. Specifically for ambush and cursorial spiders, the type of substrate is also very relevant because spiders often rely on substrate-borne vibrations to find their prey, and distinct substrates propagate vibrations differently. At this point or after contacting the prey, spiders have to decide whether or not to attempt capture. Such a decision involves profitability, prey defenses, and the physiological state of the spider. To capture prey, ambush and cursorial spiders may rely on web sheets, adhesive setae on the tips of the legs, glue-spitting, and venom directly injected from the fangs of the chelicerae. The actual mode of ingestion also varies among species. For almost every step from picking a foraging place to prey consumption, multiple sensory modalities may be used, such as vision, contact chemoreception, olfaction, detection of substrate-borne vibrations, and air displacement. Adequately choosing where to forage, properly detecting, choosing, capturing, and handling prey may have important fitness implications. In this chapter, we summarize the knowledge on these topics with regard to Neotropical cursorial and ambush spiders, detecting gaps and areas better covered within the topics above. Finally, we attempt to suggest promising model species to investigate these different steps of foraging in these animals.

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Spiders are a diverse group of predators, and their evolution has been accompanied by the evolution of their main prey, insects (Vollrath and Selden 2007). Strategies for searching out and capturing prey vary greatly among spiders, which may prey upon flying, running, walking, jumping, and even aquatic prey. Cardoso et al. (2011) classified how spiders exploit resources in different guilds or functional groups. Within spiders, some species use webs to attract and capture prey (“sensing web”, “sheet web”, “space web”), but others do not use webs and rely mainly on their legs and chelicerae to immobilize prey. Many of these spider families fall within the guilds of “cursorial hunters”, “ambush hunters” and “other hunters” (Cardoso et al. 2011). Among spiders, the guild of “ground hunters” consists of 19 Neotropical families, including Lycosidae, Oonopidae, Corinnidae, and Paratropididae, among others. The guild of “ambush hunters” comprises six families, five of which occur in Neotropical regions: Deinopidae, Thomisidae, Microstigmatidae, Sicariidae, and Selenopidae. In the “other hunters” guild, the authors included the Neotropical families Clubionidae, Senoculidae, and Ctenidae, among others. Spiders with “uncommon” predatory habits, such as the species of Scytodidae, which spits on prey to capture them, are also in this group (Cardoso et al. 2011).

In this chapter we describe through a discussion of diet how non-web-building spiders manage to acquire food; the choice of an adequate site to forage; and detecting, capturing, and handling prey, emphasizing Neotropical species. Because in many cases there are no examples of Neotropical species, we often refer to studies conducted in the Northern Hemisphere. We aim to provide complementary information to great previous reviews of spider foraging such as the book chapters by Riechert and Luczak (1982), Romero and Vasconcellos-Neto (2007), and Nelson and Jackson (2011), and the classic book *Biology of Spiders* by Foelix (2011).

A Brief Introduction to Spider Diet

Spider diet certainly varies greatly (Fig. 9.1), ranging from polyphagous species to oligophagous and monophagous ones (Nyffeler 1999; Nelson and Jackson 2011). Detailed studies of diet breadth are sometimes done in the laboratory because the percentage of feeding spiders in the field varies from 0.4% to 8% (references in Nentwig 1986). Some spiders may feed on nectar (Salticidae: Jackson et al. 2001; Carvell et al. 2015) and some may scavenge (Sicariidae: Sandidge 2003; Cramer 2008; Vetter 2011). Spiders that feed predominantly on ants, or are specialized in woodlice, in other spiders, or in blood-fed mosquitoes, are dealt with in Chap. 10.

Polyphagous species do not just eat anything. Several factors are known to influence spider diet. The ontogeny of the spider may influence prey taxa, diversity, and size in the diet (Bartos 2011). In addition, cannibalism is common (Rypstra and Samu 2005), more often involving juveniles (Wise 2006), and more likely to occur in hungry individuals (Samu et al. 1999; Mayntz and Toft 2006; Wise 2006), which may change their locomotor activity compared with well-fed spiders (Walker et al. 1999). Finally, sexual cannibalism has also been observed in several species (e.g., Schwartz et al. 2014; Toft and Albo 2016).

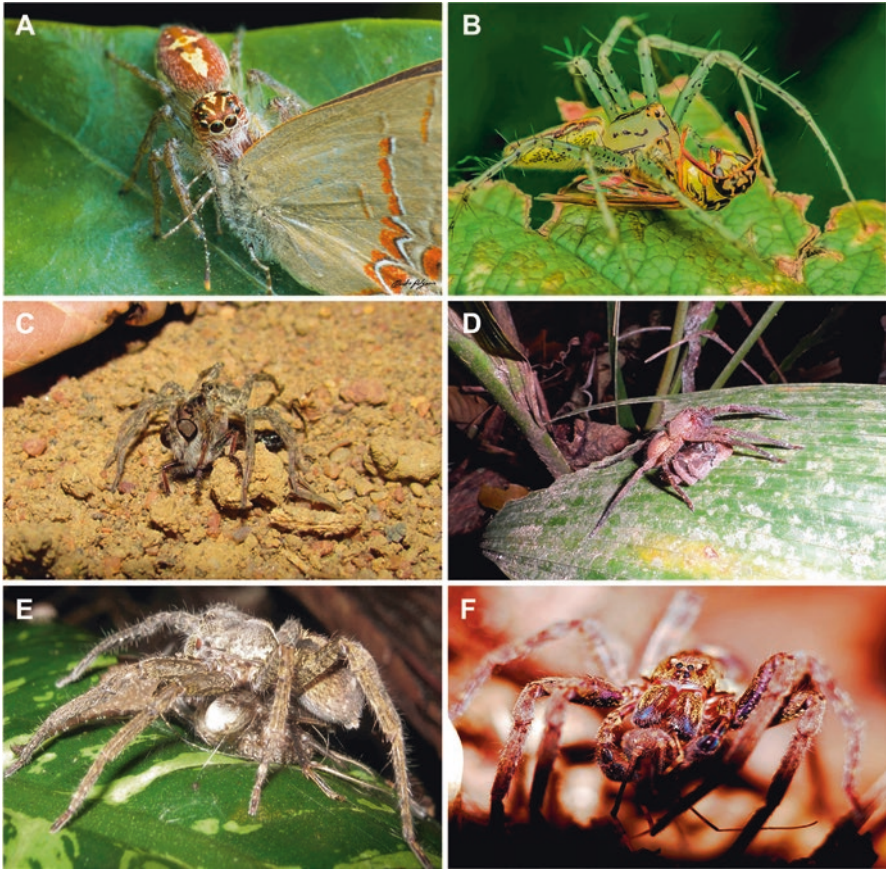


Fig. 9.1 Prey items captured by some Neotropical spider species. (a) Salticid feeding on a moth (by O. Pulgarín). (b) *Peucetia* sp. (Oxyopidae) feeding on a vespid wasp (by O. Pulgarín). (c) Lycosid feeding on an asyloid fly. (d) *Ctenus* sp. feeding on a conspecific. (e) *Ctenus* sp. feeding on a gryllid: the spider can capture a prey without releasing the previous catch (by L. F. Garcia). (f) *Ctenus* sp. feeding on a manaosbiid harvestmen (by L.F. Garcia)

Prey-to-predator size ratio matters, and spiders' prey may vary a lot in size (Erickson and Morse 1997). They tend to attack prey smaller than themselves, often less than two-thirds their size (Henschel 1994). However, prey twice the size of the spider can also be subdued (Salticidae: Bartos 2004; Thomisidae: Guseinov 2006).

Spiders may also select prey according to nutrient composition and, which is maybe more impressive, selectively ingest protein or lipids from a prey item according to its own nutritional status (Mayntz et al. 2005). Eating selectively may be very important, and feeding indirectly on nectar (by eating prey that fed on nectar), for example, may increase survival, growth, and fecundity in *Cheiracanthium inclusum* (Taylor and Pfannenstiel 2009). In *Schizocosa*, spiders with a high-quality diet mature faster, are larger, and have better body condition indexes than spiders fed on

a low-quality diet (Hebets et al. 2008). Long-term diet may affect some traits associated with mating success also in *Schizocosa stridulans* (Rosenthal and Hebets 2015). In *Paratrechalea ornata*, males in good condition may have higher mating success than males in poor condition (Albo et al. 2014). Finally, past diet influences future prey choice (Schmidt et al. 2012). Foraging in spiders is therefore a complex matter, and these animals are by no way generalists that just eat the first animal they find. There is a high interspecific variation, and prey choice is really important.

Diet in Neotropical Spiders

Ctenidae is the most studied Neotropical family of cursorial spiders when it comes to foraging and behavior as a whole. They are medium to large spiders that wander or sit and wait on trees and on leaf litter depending on the species, with males often wandering more than females (Schmitt et al. 1990; Schuster et al. 1994; Salvestrini and Gasnier 2001; Gasnier et al. 2002). *Ctenus*, *Cupiennius* and *Enoploctenus* leave their retreat at night, preying upon cockroaches, crickets, earwigs, flies, grasshoppers, moths, termites, and *Ctenus* spiders (Barth and Seyfarth 1979; Hofer et al. Höfer et al. 1994; Willemart and Kaneto 2004). *Enoploctenus cyclothorax* was found to usually reject the armored harvestmen *Mischonyx cuspidatus* (Willemart and Kaneto 2004), and Willemart and Pellegatti-Franco (2006) found that almost 80% of the spiders rejected this harvestman even after having been starving for more than 2 months. In contrast, crickets offered simultaneously for control spiders were all eaten within 13 h. It was later found that the cause of rejection is probably the thick exoskeleton of armored harvestmen (Laniatores) as a whole (see below).

Few Neotropical cursorial species have had their diet studied in detail. Nentwig (1986) studied the diet of seven species of cursorial spiders in the laboratory. He offered a variety of prey. Relatively softly chitinised insects (Diptera, Lepidoptera, Homoptera, Miridae, Ensifera) had acceptance rates of more than 50% by spiders of the families Lycosidae, Thomisidae, Salticidae, and Linyphiidae. Arthropods with a thick cuticle (e.g., Coleoptera) and arthropods that are aggressive and/or are chemically defended (e.g., Formicoidea, many Heteroptera, Myriapoda) were mainly refused. The large *Cupiennius* was an exception, accepting sometimes chemically defended and armored prey. Nentwig (1986) has shown that *Cupiennius* (Ctenidae) is at the polyphagous end of the spectrum, and *Misumena* (Thomisidae) was the most specialized studied species, with *Pisaura* (Pisauridae), *Evarcha* (Salticidae), *Xysticus* (Thomisidae), *Pardosa* (Lycosidae), and *Tibellus* (Philodromidae) in between, in this order. Nentwig (1986) suggests that the degree of polyphagy is influenced by the spider habitat and the availability of prey. For example, whereas *Cupiennius* has a large array of prey items available in the forest, *Tibellus* in meadows and *Misumena* on flowers have a less diverse array of prey available.

Thomisids (popularly known as crab spiders) are commonly found on flowers where they wait for prey. Romero and Vasconcellos-Neto (2003) found that the crab spider *Misumenops argenteus* feeds on a variety of insects that visit the flowers it

forages on (Asteraceae). The authors have observed 76 spiders feeding in the field, and prey consisted of herbivores (43.5%), pollinators (8%), parasitoids (12%), and predators (23%). The rest were other arthropods. Although *M. argenteus* is polyphagous, it attacked mostly prey that stayed longer on the plant (such as prey that got stuck within the trichomes of the leaves) or wingless insects (Romero and Vasconcellos-Neto 2003).

The spitting spider *Scytodes longipes* (“other hunters” guild) is a polyphagous species that exhibit preferences based on prey morphology. This synanthropic species with a body length of 10 mm in captivity studies show a great preference for Ensifera and other spiders as a prey. They refuse hard-chitinised prey such as beetles, and dangerous prey such as bees and wasps and prey larger than 24 mm (Nentwig 1985). Differently from the spitting spider, the diet of the recluse spider *Loxosceles* includes hard-bodied prey such as beetles and isopods, and dangerous prey such as ants (Fischer et al. 2006; García et al. 2016). Other species known to include ants in their diet are the sand-dwelling spiders *Allocosa alticeps* and *A. brasiliensis* (Lycosidae) (Aisenberg et al. 2009). The remaining prey items consumed are insects, mainly beetles and dipterans, the latter being caught mainly during their nuptial swarms. The authors suggest that these *Allocosa* are actually opportunistic feeders (Aisenberg et al. 2009).

Lycosids may also possibly prey upon vertebrates. Though vertebrates are often considered as spider predators and not as their prey, spiders from several families, including Ctenidae, Pisauridae, Trechaleidae, Lycosidae, Sparassidae, and mygalomorphs were observed consuming this prey category. Theraphosids, for example, were observed preying upon several species of anurans and caecilians (Menin et al. 2005), snakes (Borges et al. 2016), and lizards (Vieira et al. 2012). Arboreal species of the genus *Avicularia* have been observed preying on small mammals such as bats (Nyffeler and Knörnschild 2013). Because *Ctenus* and *Ancylometes* are very abundant on the forest ground in Amazonia, Menin et al. (2005) have suggested that predation on vertebrates by spiders is ecologically important. Finally, there are several records of large ctenid and trechaleid spiders preying on various species of fish and anurans (Höfer and Brescovit 2000; Zina and Gonzaga 2006; Nyffeler and Pusey 2014).

Choice of Foraging Site

When food resources become scarce, spiders are at risk of starving if they stay at the same locality for a long time. This is often a determining factor triggering displacement to another site (Wagner and Wise 1997). In two North-American species of the genus *Pardosa* and *Hogna*, experiments showed that well-fed individuals have a lower mobility when compared with starved individuals (Walker et al. 1998). Once the spider arrives at a new locality, it must evaluate several factors before deciding to stay there, including the presence of prey and predators. The decrease in foraging activities in the presence of predators is a common

behavior in several animals including spiders. Eiben and Persons (2007) evaluated the effect of vibrations, chemical and visual cues of the predatory North American lycosid spider *Pardosa milvina* on the activity of another lycosid *Rabidosia rabida*. The predator cues, mainly chemical ones, inhibited the activity of *R. rabida*. *Pardosa* in turn, are preyed upon by the larger *Hogna*. *Pardosa* discriminates the quantity of predatory cues and how old the cues are, behaving accordingly (Persons and Rypstra 2001; Barnes et al. 2002; Rypstra et al. 2007). Predator diet also matters: cues from the larger spider *Hogna* fed the smaller *Pardosa* elicited a significantly greater reduction in activity in *Pardosa* than *Hogna* fed crickets (Persons et al. 2001). Moreover, *Pardosa* have been shown to avoid pitfall traps with *Hogna* but did not avoid empty traps or traps with crickets, indicating the important role of olfaction (Schonewolf et al. 2006).

The presence of prey or prey cues when choosing a foraging site also matters. The spider *Pardosa ramulosa* is more frequently found next to pools of water with aquatic insects such as dipteran larvae (*Aedes* and *Ephydra*) and the heteropteran *Trichocorixa*, common prey for these spiders (Greenstone 1983). The European wolf spider *Pardosa saltans* chooses foraging sites containing silk and feces left by smaller spiders and conspecifics, both potential prey (Wetter et al. 2012). The North-American wolf spider *Schizocosa ocreata* remains longer when exploring sites with cricket cues (Persons and Uetz 1996). Chemicals may sometimes repel spiders: individuals of *Pisaura mirabilis* move away from different extracts of flowers that contain b-caryophyllene and nerolidol. However, the thomisid *Misumena vatia* that usually forages on flowers is not repelled by these chemicals (Junker et al. 2011).

The substrate to wait for prey is also considered by spiders. The thomisid *Misumenops argenteus* prefers flowers of *Trichogoniopsis adenantha* that match the spider colors (Heiling et al. 2005). Romero (2001) showed that this spider occurs most frequently on this plant when compared to other plants in the same environment. These flowers also offer a wide variety of prey to the spider by attracting different phytophagous insects such as heteropterans, orthopterans, aphids, and lepidopterans, though also parasitoids such as Braconidae and Pteromalidae (Romero and Vasconcellos-Neto 2003). Nevertheless, because some pollinator insects avoid flowers with crab spiders (Heiling et al. 2003; Dukas and Morse 2005; Gonçalves-Souza et al. 2008; Romero et al. 2011; Llandres and Rodríguez-Gironés 2011), and assuming that predators may also do it, an alternative hypothesis is that the flower color choice is actually an antipredatory behavior.

Specifically when ambush prey, the type of substrate is also relevant because cursorial spiders often rely on substrate-borne vibrations to find their prey, and distinct substrates propagate vibrations differently. Some Neotropical ctenids, such as *Cupiennius salei*, prefer to forage on leaves of banana plants, which are good conductors of vibrations produced by prey (Barth et al. 1988; Barth 2002). Finally, habitat complexity may negatively affect prey capture in *Pardosa milvina*, but it offers protection against the large spider *Hogna helluo* (Rypstra et al. 2007). Therefore, a good foraging site is definitely not a randomly chosen one but depends on the physiological conditions of the spider, presence of prey and predators or their cues, adequate substrate, and habitat complexity.

Prey Detection

Spider legs, in addition to being used in locomotion, prey capture, mating behavior, and web building, possess various receptors of external stimuli (Foelix 2011). One of the main receptors is the trichobothrium, a structure located on the tarsi, metatarsi, and tibia of pedipalps and legs (Barth 1982). A trichobothrium is usually a long and thin hair that emerges from a socket with sensory cells connected to the base of the hair (Reissland and Görner 1985). About 900 trichobothria can be found on the legs and pedipalps of the ctenid *Cupiennius salei* (Barth and Holler 1999). Because groups of trichobothria may be arranged in different spatial combinations and because the length of the hair shafts are variable, they respond to a wide range of wavelength frequencies, including vibrations produced by some flying insects such as flies that tend to be very turbulent and easily detectable (Barth 2002). Other important sensors for detecting prey are the metatarsal lyriform organs, which are slit sensilla located on the distal region of the metatarsus. The slit sensilla are areas with thinner cuticle in the exoskeleton that are very susceptible to deformations (Young et al. 2014), which are readily detected and transmitted to the nervous system (Barth et al. 1993).

The Neotropical spider *Cupiennius salei* has been used as a study model of receptors and sensory organs (Barth 1985, 2002, Patil et al. 2006b; McConney et al. 2009; Young et al. 2014), providing most of the information we know about trichobothria and metatarsal lyriform organs. The intensity of the vibrations produced by the movements of the prey varies with the distance and therefore indicates how far the prey is from the spider (Hill 2009). In addition, spiders only respond to some of a range of vibrational cues, and can distinguish between vibrations produced by conspecifics of the opposite sex from other sources such as abiotic factors (wind) or potential prey (Barth 2002; Hill 2009).

Olfactory receptors are also present in spiders, being located on distal parts of the legs and pedipalps, in a structure called the tarsal organ, which encloses six or seven innervated sensilla with a pore at the tip (Foelix and Chu-Wang 1973). During prey detection, olfactory receptors have been shown to play a role. The spider *Cupiennius salei* (Hostettler and Nentwig 2006) is able to distinguish between cricket gel models with and without cricket smell, preferring those with scent, suggesting these spiders use olfactory cues for prey detection. Another example is *Falconina gracilis* (Coriniidae), which is able to detect the pheromones produced by its prey, the ant *Acromyrmex landolti fracticornis* (Fowler 1981).

Visual cues can also be used for prey choice and capture behavior. Spiders generally possess eight eyes that are arranged in pairs and named according to their positions: anterior median, anterior lateral, posterior median and posterior lateral eyes. The anterior median eyes can receive and transmit more complex stimuli than other eyes (Barth 2002), having sometimes extraordinary spatial resolution. That is the case with spiders in the family Salticidae, which have anterior median eyes much larger than the other eyes. The African jumping spider *Evarcha culicivora* is able to visually distinguish *Anopheles* mosquitoes which recently fed on

vertebrate blood from *Anopheles* which did not feed on blood, and to distinguish *Anopheles* from *Culex* by their posture when resting (Jackson et al. 2005; Nelson and Jackson 2006, 2012). With regard to prey capture, *Corythalia albicincta* jumps on the prey from a greater distance (~2.5 times its body length) when dealing with fast-moving crickets or adult flies compared to fly larvae (~1 time its body length) (Aguilar-Argüello and García-Chávez 2015). These jumping spiders also behaved differently when dealing with different prey: the latency to jump on larvae is higher, maybe because they do not move as much as the other two insects used as prey items. These behaviors are probably possible because of salticid's great vision. Other spiders that rely on vision for prey capture are the ogre-faced spiders (genus *Deinopis*). These are commonly seen at night in Neotropical forests holding their nets waiting for prey. Getty and Coyle (1996) have described the prey-capture behavior of these amazing spiders. They may either strike forward to capture wandering prey or backwards towards mechanical stimuli (vocalizations or vibrating tuning forks, aerial strikes). *Deinopis* has recently been found to also rely heavily on its posterior median gigantic eyes to capture prey (Stafstrom and Hebets 2016). Interestingly, another nocturnal species, *Cupienius salei*, which is known to heavily rely on mechanical stimuli to detect prey and does not have particularly large eyes, may also use its eyes to detect movement and attack (Fenk et al. 2010). In lycosids, visual information may also influence patch residence time (Persons and Uetz 1997).

There is therefore evidence of spiders using an array of sensory stimuli to detect prey, including air- and substrate-borne vibrations, volatiles, and visual stimuli. We do not know much about the interaction and relative importance of these sensory modalities in Neotropical spiders for detecting prey. However, studies on salticids, lycosids, and ctenids mentioned above have shown that these animals can definitely use more than one sensory modality when foraging.

Prey Capture with Emphasis on Neotropical Spiders

Most predators try not to be detected by their prey, and camouflage may therefore be useful: the light-colored salticid *Yllenus arenarius* attacked from closer distances, approached prey faster, and was more successful when camouflaged in light substrates than in darker ones (Bartos et al. 2013). However, other species do the opposite and actually expose themselves to attract prey, sometimes exploiting the sensory system of their prey: crab spiders hunting honeybees on flowers may attract prey with UV reflectance on their bodies (Llandres and Rodríguez-Gironés 2011). The white patches on the forelegs of *Dolomedes raptor* also attract prey: dummies with patches attracted more grasshopper prey than dummies without the patches, and grasshoppers were more attracted to spiders when their white patches were present (Tso et al. 2016). After prey attraction, spiders need to efficiently attack and hold them. Holding prey requires adhesive setae on the ventral region of the legs in

some species, with the predator jumping on the prey with the legs forming a basket that involves the prey (Lycosidae: Rovner 1980). In contrast, *Scytodes* immobilize prey by spitting a mixture of glue, silk, and venom from the chelicerae (Suter and Stratton 2005). Horizontal web sheets may also be used in cursorial species such as the recluse spider in the genus *Loxosceles* (Cramer 2015). Behaviors displayed when capturing prey may vary depending on the prey and ontogenetically in the speed, direction of approach, and prey manipulation among others (Bartos 2007, 2008; Pekár and Lubin 2009; Pekár and Haddad 2011; Bartos and Szczepko 2012).

Animals have to save energy whenever possible if food availability is unpredictable. *Cupiennius salei* can control the amount of the costly venom they inject when subduing prey according to the size of the prey and the intensity and duration of struggling movement (Malli et al. 1998, 1999). Prey items that are easier to capture such as stick insects and crickets receive less venom than blowflies and beetles, which are harder to subdue (Wigger et al. 2002). Moreover, individuals of *C. salei* are aware of the amount of venom available in their glands: when experimentally venom-depleted, they orient towards prey less often and display a decrease in their attack rates (Hostettler and Nentwig 2006). Moreover, they choose prey accordingly. Prey more sensitive to their venom are preferred over prey less sensitive when their glands are experimentally emptied (Wullschleger and Nentwig 2002). What is even more amazing is that they can make such choices using olfaction only (Hostettler and Nentwig 2006). This ability to control venom use according to each prey makes sense in the diverse Neotropical forests where these spiders live, where a wide array of prey are available for this polyphagous species. If there is a relationship between stenophagy and euryphagy and venom control, we could predict that specialized spiders such as some dysderids (woodlouse eaters) or salticids (spider eaters) would vary less the amount of venom injected in their prey.

Dealing with Dangerous Prey

Biting may require extra care when spiders are dealing with well-defended prey such as arthropods that are chemically defended. The chemical defenses used by harvestmen (Arachnida, Opiliones), if experimentally applied to a palatable prey, may repel trechaleid and ctenid spiders (Machado et al. 2005), which sometimes drop the prey and rub their mouthparts against the substrate after contacting the defensive droplet (but see Souza and Willemart 2011: *Enoploctenus cyclothorax* did not release prey after contacting the secretion of *Discocyrtus invalidus*). The predation strategy of recluse spiders (*Loxosceles*) is more efficient in avoiding defensive secretions because the spider bites only the legs of these harvestmen, therefore decreasing the chances of coming into contact with their defensive secretions (Segovia et al. 2015a).

Some armored harvestmen in the suborder Laniatores have dangerous sharp spines on legs IV that can pierce a spider abdomen (Segovia et al. 2015b). Such

pinching with legs IV startles large ctenids: they may move away from the prey even when the spines do not touch the spider (Dias et al. 2014). *Loxosceles*, however, carefully approach such armored harvestmen, avoiding proximity with legs IV, spiny pedipalps, and chelicerae of these prey (Segovia et al. 2015a). In a spider-spider interaction, the spitting spider *Scytodes globula* occasionally invades webs of other spiders such as *Metaltella simony* to prey upon them. However, the host spider may react defensively and make the spitting spider spit defensively, aborting the attack (Escalante et al. 2015).

Whereas ants are often avoided by some spiders, others include ants in their diet. That is the case of *Loxosceles*, polyphagous animals that efficiently subdue these dangerous prey (García et al. 2016). However, some spider species actually specialize in ants. The aphantochilid *Aphantochilus rogersi* in late instars preferentially attacks ants from behind, probably avoiding their dangerous mandibles (Oliveira and Sazima 1984; Castanho and Oliveira 1997). Younger specimens use a different strategy because probably they can only seize the ant's petiole tightly if they approach the ant from the front (Castanho and Oliveira 1997). While spiders are eating, patrolling ants may pass nearby and occasionally approach the spider, which raises the dead ant and shows it to the approaching ant, as if it were an ant carrying a dead nest mate (Oliveira and Sazima 1984). The morphological similarity between *A. rogersi* and their model ants of the tribe Cephalotini, however, is thought to help them avoiding predation, since visually guided predators often avoid ants (Oliveira and Sazima 1984).

Dealing with Prey Armor

Some arthropods with a hard exoskeleton are sometimes rejected by spiders after these touch the prey (Nentwig 1985; Eisner et al. 2004; Carvalho et al. 2012; Souza and Willemart 2013; Dias and Willemart 2013). Because laniatorid harvestmen are well protected within a rigid armor, spiders that bite in random areas of the prey have low success (successful captures: *Enoploctenus cyclothorax* 2/40, *Ctenus ornatus*: 5/34) (Souza and Willemart 2011; Dias and Willemart 2013). The spitting spider *Scytodes globula* has been shown to never overcome prey defenses (0/33) (Carvalho et al. 2012). In contrast, the recluse spider (*Loxosceles gaucho*) only bites the non-sclerotized distal parts of the legs and the soft articulations. It successfully killed and ate armored harvestmen in 31/38 opportunities (Segovia et al. 2015a). The scorpion *Bothriurus bonariensis* stings at the mouth, another soft part of a harvestman's body. Its success was 35/58 (Albin and Toscano-Gadea 2015). The spider *Ctenus fasciatus* is known to feed on Goniosomatinae harvestmen in caves (Gnaspini 1996), contrasting with studied ctenids that are often unsuccessful when attacking armored harvestmen (Souza and Willemart 2011; Dias and Willemart 2013). Prey capture has not been studied in *Ctenus fasciatus*, but its strategy is possibly similar to that of other ctenids: jumping on the prey, sometimes manipulating it a bit and biting in random areas. However, because *C. fasciatus* are very large, heavy-bodied,

and have big chelicerae, they possibly overpower the armor by simply breaking it with their fangs, which *E. cyclothorax* rarely manages to do and *C. ornatus* only occasionally does.

Some spider species included in the families Lycosidae, Trechaleidae, and Ctenidae quickly jump on the prey and bite it. However, spiders such as *Scytodes* and *Loxosceles* (Ades and Ramires 2002; Segovia et al. 2015a; García et al. 2016) carefully approach and tap prey before spitting venom or biting. We know nothing about what information these spiders are accessing when tapping prey. Spiders do have contact chemoreceptors on their legs, but are they accessing prey chemicals in order to decide whether or not to continue attacking? If they are, we could be able to experimentally fool these spiders by applying chemicals of other animals such as mates or predators. Is contact required to identify prey or only to search for vulnerable areas to bite? Why do some spiders tap prey, while others do not and simply jump on the prey? With regard to the adhesive hairs needed to hold prey after jumping on it (Rovner 1980), we know autotomy brings costs to foraging spiders by reducing capture rate in complex environments (Wrinn and Uetz 2008). Since many legs are used for holding prey (Rovner 1980), is it possible that autotomy affects capture success (Amaya et al. 2001)? Do ctenids or lycosids have more adhesive hairs than sicariids or scytodids? These and several other questions remain still unknown.

Handedness in Spiders?

Laterality is common in animals, both invertebrates and vertebrates, including humans (see references in Benelli et al. 2015). Gorillas may be right-handed for most of their frequent intraspecific gestures (Prieur et al. 2016), left-handed humans may be favored for example by their surprise effects when fighting the majority of right-handed fighters (Pollet et al. 2013), and octopuses may use one eye more than the other to look at stimuli using monocular vision (Byrne et al. 2004). Cesar Ades, one of the researchers responsible for the spread of ethological studies in Brazil, with his former student Eduardo Ramires, provided evidence that spiders may also have behavioral lateralization (Ades and Ramires 2002). The authors first detected that *Scytodes globula* collected in the field were missing left legs I and II more often than right legs I and II. Knowing that these spiders usually attack after touching the prey, the authors hypothesized that they use left legs more often than their right counterparts to tap prey. They brought *Loxosceles* to the laboratory to use them as prey and, indeed, when *Loxosceles* managed to bite a leg of *Scytodes*, the latter autotomized the leg caught. In one case where the spider did not autotomize the leg, it died. Their results showed that *Scytodes* as a whole used their left legs I and II more often than the right legs I and II to probe prey. Though the authors could not provide a clear explanation as to why lateralization occurs, the results were clear and the first example of lateralization in arachnids. As suggested by the authors, it would be nice to know whether there is an individual consistency in handedness.

Should We Expect Differences in Foraging in the Neotropics Compared to Temperate Regions?

Before we start discussing this question, we have to bear in mind that the Neotropical region encompasses very distinct ecosystems, with differences in biotic and abiotic factors. We are grouping Patagonia, where temperatures may reach -15 Celsius in winter, with Manaus in the Amazon rainforest where temperatures are rarely under 20 °C and often above 30 °C. However, the Neotropical region that is actually between or close to the tropics is fairly different from temperate regions as a whole, for example. We can therefore attempt to extract potentially useful information in an attempt to understand different selective pressures that may influence foraging.

Moya-Laraño (2010) proposed that higher temperatures and water availability (which is often the case in the tropics) could permit higher rates of mobility in organisms, maybe leading to higher rates of encounter among individuals. This could lead to the prediction that spiders in Neotropical forests would wander more than spiders in temperate forests. However, spiders are prey to a diverse array of predators among invertebrates (including other spiders) and vertebrates (amphibians, reptiles, mammals), which are both more diverse in the tropics than in temperate regions. Moreover, there is evidence at least in invertebrates and fishes that predation pressure increases toward the tropics (Schemske et al. 2009). This would lead to the opposite prediction; that spiders should wander less in the tropics to avoid predation. Of course, other factors should also be considered: for example, higher temperatures per se may increase the locomotor activity of wandering spiders (Ford 1978), which may bias comparisons between temperate and tropical forests.

Several spiders in temperate regions overwinter as immature or adults in areas where temperature may be well below 0 °C. They deal with such conditions by choosing appropriate microhabitats, increasing resistance to cold or reducing their metabolic rate (Foelix 2011). Some long-lived spiders in temperate regions, such as *Dolomedes* (Pisauridae), may take 2–3 years to become adults in northern regions of their distribution (Jones et al. 2001). Individuals of *Pardosa lugubris* (Lycosidae) in Scotland or Netherlands may need 2 years to become adults in nature (Jones et al. 2001). That means they overwinter as immature, dealing with very low temperatures in winter. Do low temperatures influence foraging? In two species of crab spiders (Thomisidae) from New Jersey (USA), there is no relationship between the number of prey captured in the field and temperature, controlled per prey type (Schmalhofer and Casey 1999). With laboratory experiments, Schmalhofer and Casey (1999) also asked whether temperature affected the hunting performance (HP) of these spiders on flies. They measured HP in the laboratory according to the equation: $HP = ab/c$, where “a” indicates whether or not a spider made a kill (yes = 1, no = -1), “b” is the number of strikes made by a spider, and “c” indicates the number of opportunities the spider had to strike at prey. It is important to state that such a formula does not directly evaluate physiological

effects of temperature but only the final outcome, that is, what the spider actually ingests. The authors have shown that temperature did not influence HP, which they attribute to muscle physiological adaptations for burst activity and/or the use of venom. Hunting performance being unaffected is important not only because of daily variations but also because of seasonal variations, allowing these crab spiders to maintain feeding rates also in the reproductive season, when temperature declines for one of the species studied. Foraging success is correlated with reproductive success also in crab spiders (Morse and Stephens 1996). We can ask if foraging thomisids in the Neotropical region, where the spiders do not have to deal with such low temperatures, are also unaffected by temperature. Or is it an adaptation to areas with greater temperature variation? Similar tests could be done comparing pisaurids and lycosids from temperate and Neotropical regions. We do not know much about this topic in Neotropical species, but in some warm desert web-building species, low temperatures may affect latency to attack, duration of prey-capture sequences, web mass, and time allocated to feeding in spiders in the families Eresidae, Theridiidae, and Agelenidae (Riechert and Tracy 1975; Lubin and Henschel 1990; Henschel et al. 1992; Turner et al. 1993). Spiders may also thermoregulate behaviorally (Humphreys 1978, 1987), which can also influence metabolism and therefore foraging, but this is widely unexplored in spiders. While most studies on the influences of temperature on behavior and physiology in arthropods have been conducted in insects (Chown and Nicolson 2004), the wide distribution of some spiders certainly contributes to studies comparing latitudinal effects of temperature on foraging behavior.

Concluding Remarks

Hunting spiders are widely distributed and present a high diversity in the Neotropics, also comprising a wide diversity of feeding strategies. When compared to the temperate regions, knowledge about feeding behavior on Neotropical spiders is scarce, since there are few studied species and in some cases the same species is used as a model for many studies, such as *C. salei*. Additionally, research on Neotropical hunting spiders has focused mainly on sexual and reproductive behaviors, while studies about feeding behavior are still lacking. Neotropical hunting spiders are good models for the study of predatory behavior because they include a wide variety of prey from small or dangerous insects such as ants, up to vertebrates such as bats. They also play an important role as predators of different ecosystems such as crops (see Chap. 11), and are suitable models for the study of evolutionary and ecological questions, and also of applied problems related to trophic ecology. All these characteristics call for the need to intensify studies of the predatory behavior of these spiders.

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