

Attacks on very large and dangerous prey by jumping spiders (Araneae: Salticidae)¹

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Some years ago Robinson & Valerio (1977) described *attacks on large or heavily defended prey* by salticid spiders. They found that dropping on the dragline while holding their prey gave these spiders the ability to safely handle them. To this can be added several additional features of the salticid attack that give many species the ability to handle even *very large and dangerous prey* (Table 1).

Table 1. Some abilities that allow salticid spiders to attack very large and dangerous prey.

	ability	how it works
1	detailed view of prey anatomy	can avoid the defenses of the prey with a targeted attack in the best direction
2	slow approach to jumping position	In some cases cryptic movement is used to avoid detection
3	jumping attack at a distance	gives the attacking salticid a much greater reach than that of dangerous or raptorial prey
4	speed of jump (~80-cm/s take-off)	faster than the reaction time of prey
5	use of gravity to accelerate attack	By jumping down the range of attack can exceed 10 cm, and the attack is accelerated by gravity
6	accurately target head or neck	With (1), avoids defenses of the prey
7	attack with the fangs	Strong, piercing fangs with a serrated edge can securely penetrate cuticle and hold prey
8	injection of venom	Venom can include a mixture of fast-acting components to induce paralysis and necrosis
9	brake and rebound on the dragline	Braking on the dragline leads to elastic rebound on the dragline, pulling prey up and away
10	hold prey while suspended on dragline	With no foothold struggling prey cannot effectively grapple with the attacking salticid
11	autonomy of leg when bitten	If bitten during an attack, a salticid can autonomize the affected leg to limit the effect of venom

This repertoire allows salticids, and larger salticids in particular, to capture large (near their size) or very large (much larger) prey without having to grapple with that prey, a contest that the salticid would almost certainly lose. And, in fact, sometimes the salticid does lose.

Mantids (Mantoidea: Mantidae) are voracious predators that can capture small birds (Nyffeler et al. 2017a; Kolnegari et al. 2022) and lizards (Jehle et al. 1996) with their raptorial forelegs. They also have large eyes and excellent vision, including stereopsis (Horridge & Duelli 1979; Kral 2012; Rosner et al. 2020). Although sometimes captured by orb-weavers (Araneidae), they also have the ability to escape these webs and to *remove spider silk from their bodies* (Sugiura et al. 2019, 2020). They are known to prey on spiders, but their aversion to ants may protect ant-mimicking spiders (Ramesh et al. 2016).

Mantids can strike their prey quickly, but their range for these quick movements is constrained by the reach of their raptorial forelegs (Prete et al. 1990). Some jumping spiders can prey on even the larger mantids (Figure 1). An attack on a smaller mantid is apparently not a problem for some jumping spiders like *Colonus* (Figures 2, 3). The mantid is particularly vulnerable to a targeted strike to the head (Figures 1, 5). Since a decapitated mantid is still capable of considerable movement mediated by post-esophageal ganglia (Roeder et al. 1960; see Figure 5.3), one would expect to see dangerous, defensive movements by

the legs of the mantid after this kind of attack. However inhibition from centers in the first postesophageal (*subesophageal*) ganglion of the mantid (Roeder et al. 1960) may continue for some time after paralysis of brain centers.



Figure 1. Capture of a mantid by a female *Hyllus* sp. in Borneo (photo © Nicky Bay, used with permission). One large compound eye of this mantid was held securely in the fangs of this relatively large salticid, and already shows signs of necrosis. The large raptorial legs of this mantid, although much more powerful than the spines of the spider, were of no avail. Note that this *Hyllus* had no need to grapple with her prey, and her anterior lateral spinnerets are extended to the rear, most likely holding a dragline under tension. You can also see that legs R2 and R3 of this *Hyllus* have regenerated, most likely both lost at the same time, possibly during a previous attack on dangerous prey.



Figure 2. Capture of a smaller mantid (*Stagmomantis carolina*) by an adult female *Colonus sylvanus* in South Carolina (Hill 2018a, CC BY 4.0, D. E. Hill). **1**, Upon sighting the *Colonus*, the mantid began to run directly toward it. At the same time the *Colonus* prepared to jump. Attacking at a greater range, the *Colonus* grasped the mantid with her fangs in mid-air. **2**, Recoil on the dragline after this capture brought both back to the underside of the leaf (1, far left) from which the *Colonus* jumped.



Figure 3. Capture of an immature mantid by a female *Colonus cf. sylvanus*, Progreso, Yucatan, México, 29 AUG 2022 (photos © Luis Trinchan, iNaturalist observation 133278185, CC BY-NC 4.0). Note the unsuccessful attempts of this mantid to secure a foothold as it was firmly held with a bite to the prothorax by its suspended captor. **3-4**, Note that the right foreleg of this mantid was secured by the *Colonus* with legs I and II. *Colonus* usually maintain a degree of contact between the underside of their tibiae I and some part of their prey when it is first captured, and this is the site of specialized paired setae (*bulbosae*) that may have a bioelectric function (Hill 2018a). When stalking wary prey, *Colonus* may also use a back-and-forth rocking movement to conceal their movement (Figure 4).



Figure 4. Consecutive frames showing three cycles (0.5-2 Hz) of rocking motion by a female *Colonus puerperus* as she slowly advanced to capture a female *Oxyopes salticus* at the top of a grass stem (Hill 2018a, CC BY 4.0, D. E. Hill).

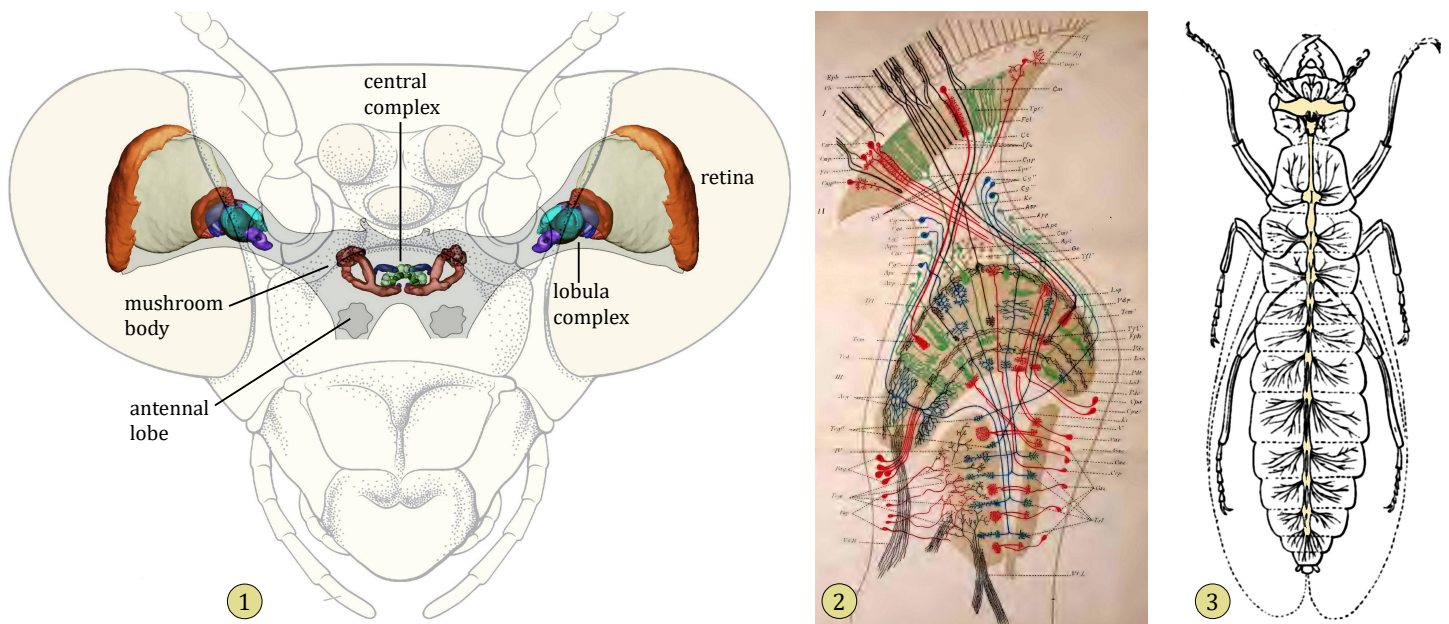


Figure 5. Given the location of the brain, the head of a mantid is particularly vulnerable target. **1**, Approximate supraesophageal position of the brain in the head of a mantid (adapted from Brannoch et al. 2017; Rosner et al 2017, 2019; CC BY 4.0, D. E. Hill). Major neuropiles, including the lobula complex of the optic lobes, are highlighted in color. **2**, Early diagram of neuronal processes associated with the optic lobe of an insect (Cajal & Sánchez 1915, CC0). **3**, Central nervous system of a primitive insect (*Corydalis cornutus*), comprised of a brain and subesophageal ganglia in the head, and a pair of ventral ganglia in each body segment (adapted from Packard 1868, CC0).

Several genera of mostly tropical salticids, including the spartaeine *Portia* (Figure 6; Jackson & Li 1996; Li et al. 1997; Jackson & Nelson 2011; Abhijith et al. 2021; Sanath et al. 2024) and the gophoine *Colonus* (Figure 7; Hill 2018a), are well-known for their stealthy approach to the spiders that they prey upon (see Figure 4). Their spider prey includes such visual hunters as thomisids, oxyopids and other salticids. Like *Portia*, spartaeines of the genus *Brettus* are also skilled at preying on web spiders *in their webs* (Jackson 2000, 2002; Abhijith & Hill 2019).



Figure 6. *Portia* preying on spiders (all CC BY-NC 4.0). **1**, *P. labiata* and prey, Taiwan, 27 JUN 2020 (photo © chonhang, iNaturalist observation 51103421). **2**, *Portia* sp. preying on *Argiope*, Hong Kong, 6 NOV 2021 (photo © slcl, iNaturalist observation 100683983). **3**, ♀ *P. labiata* and prey, Malaysia, FEB 2018 (photo © Richard Ong, iNaturalist observation 29624921).

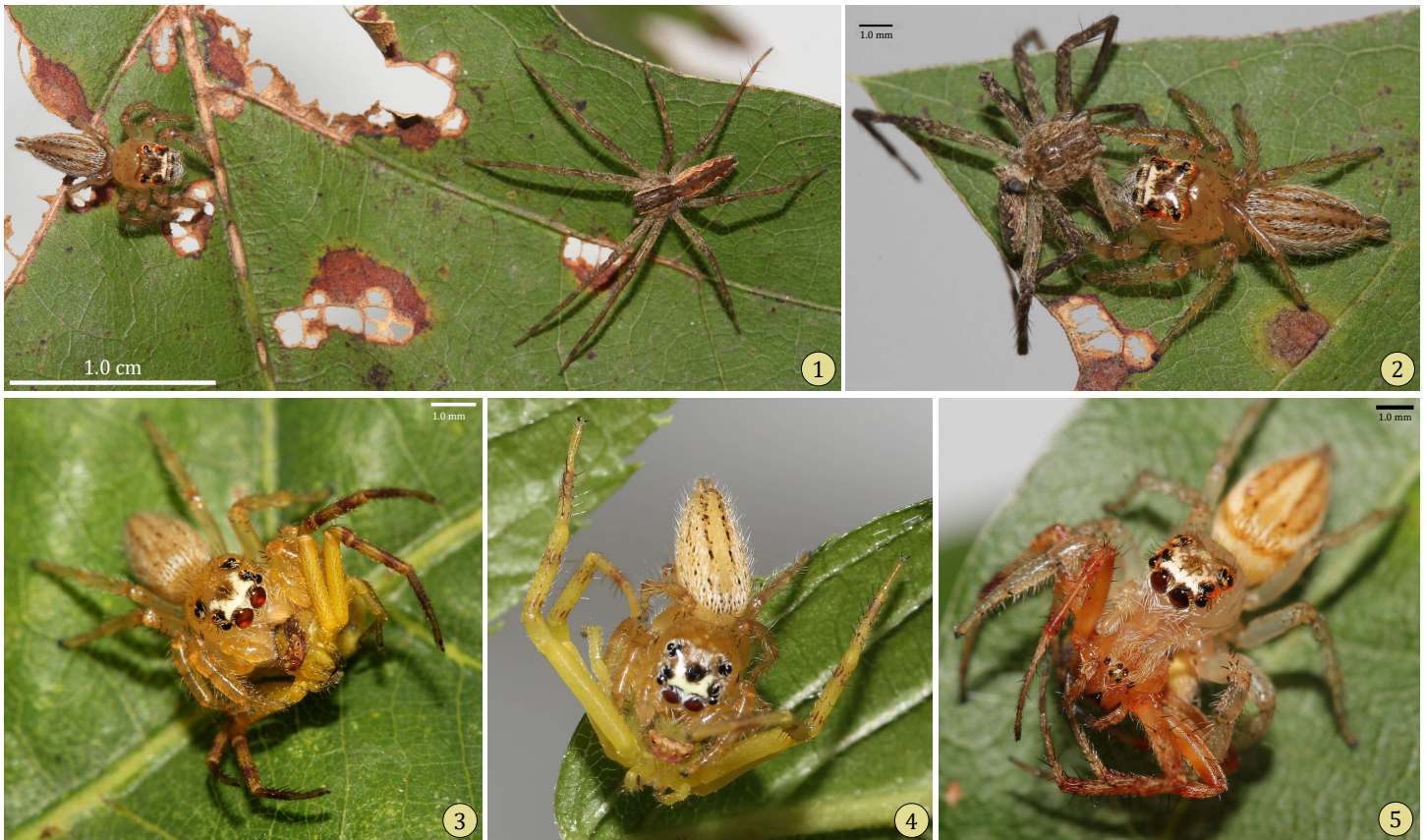


Figure 7. *Colonus* preying on spiders in the laboratory, in South Carolina (Hill 2018a, photos CC BY 4.0, D. E. Hill). **1**, ♀ *C. sylvanus* preparing to jump on a young *Pisaurina*. *Colonus* will also attack much larger adult *Pisaurina*, not always successfully. **2**, ♀ *C. sylvanus* feeding a young *Pisaurina*. **3-4**, Two different penultimate ♂ *C. puerperus* holding a thomisid (*Mecaphesa* sp.) by the rear of the carapace after jumping down to capture it. As shown in (4), the *Mecaphesa* could not reach its captor with its powerful forelegs. When these spiders sighted a *Colonus* on the same leaf, they would face the salticid and rear their forelegs in a defensive position. In these cases, *Colonus* did not make a frontal attack. **5**, ♀ *C. sylvanus* after jumping to capture an araneid by the rear of the carapace.

Many, if not most, salticids will prey on other spiders, particularly if that prey is small and immature. Even salticids like that feed primarily on ants (Figure 8) may also occasionally prey on spiders (Figure 9).



Figure 8. Members of the euophryine genus *Anasaitis*, like these *A. canosa* from South Carolina, are thought to feed primarily on ants (Edwards et al. 1974; Schadegg & King 2021; photos CC BY 4.0, D. E. Hill).



Figure 9. *Anasaitis canosa* with prey in South Carolina (photos CC BY 4.0, D. E. Hill). **1**, Feeding on a small icneumonid wasp in the leaf litter. **2**, Feeding on a theridiid spider on the side of a house.

Both spiders and ants (particularly in groups) of even a smaller size can be dangerous to a salticid, and the salticids that frequently prey on ants appear to be very careful in their approach. Some, like the Australasian *Cosmophasis bitaeniata*, even rely on chemical mimicry to survive near an ant colony (Allan et al. 2002). Many euophryines, chrysillines, and some dendryphantines (e.g., *Tutelina*) are known to prey on ants. The relationship of spiders to ants has received much attention (e.g., Jackson & Nelson 2012; Cushing 2012), and will not be considered in more detail here. More examples of salticids preying on spiders are shown in Figures 10-12. Larger and heavier salticids like the tropical Afroeurasian *Hyllus* and the North American *Phidippus* may attack much larger spiders. As with *Colonus* (Figure 7), the mode of attack appears to involve a direct bite (with the extended fangs; Hill et al. 2021) to the rear of the carapace, and the attack must be accurate. In the field I once observed a female *Colonus sylvanus* stalking an adult *Pisaurina* of much greater size. Off slightly, she was immediately grasped by her much more powerful prey, and immediately devoured. This is a dangerous business.



Figure 10. **1**, ♀ *Hyllus diardi* with captured sparassid, Rayong, Thailand (photo © Wang Chan, CC BY-NC 2.0; see also Gilman 2016). **2**, Freyine with captured spider, Puerto Inca Province, Peru, 26 SEP 2022 (photo © Dieter Schulten, iNaturalist observation 140346653, CC BY 4.0) **3**, ♀ *Phidippus clarus* with lycosid prey, Wichita, Kansas, 17 AUG 2021 (photo © Ryan Philbrick, iNaturalist observation 91564105, CC BY-NC 4.0).



Figure 11. 1, ♀ *Phidippus audax* with lycosid, South Carolina (CC BY 4.0, D. E. Hill). This salticid jumped down about 10 cm to capture this lycosid with a bite to the carapace. 2, ♀ *Thyene imperialis* with captured thomisid (*Runcinia*), Kadaramandalagi, Karnataka, 9 AUG 2013 (photo © Shashidharswamy Hiremath, iNaturalist observation 129486544, CC BY-NC 4.0).

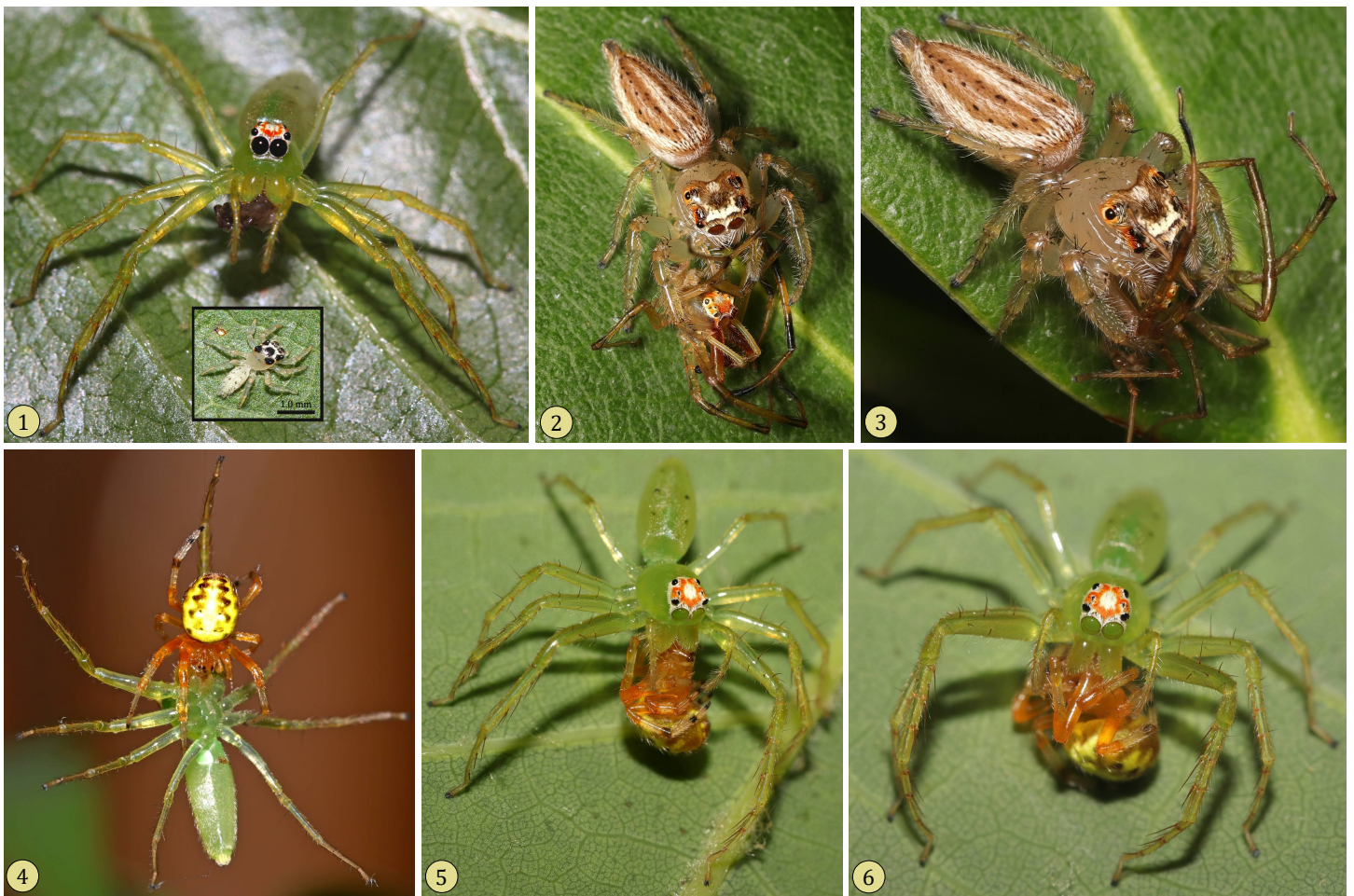


Figure 12. Field observations in South Carolina (CC BY 4.0, D. E. Hill). 1, ♀ *Lyssomanes viridis* feeding on emergent instar (II) of *Colonus sylvanus*, shown in inset. 2-3, ♀ *C. sylvanus* feeding on adult male *L. viridis*. 4-6, ♀ *L. viridis* with captured araneid.

In addition to mantids, many other insects are known to prey on spiders. These include the heavily armed robber flies (Diptera: Asilidae), although most of their prey is captured in flight (Dennis et al. 2012). But salticids can also prey on robber flies, and other large flies (Figures 13, 14.1).



Figure 13. Attacks on large and/or dangerous flies by jumping spiders. **1**, ♀ *Phidippus clarus* holding a large robber fly, Frederick County, Maryland, 13 AUG 2017 (photo © botanygirl, iNaturalist observation 8537967, CC BY 4.0). **2**, ♀ *Megafreya sutrix* holding a captured robber fly (*Blepharepium* sp.), Dique Luján, Buenos Aires, Argentina, 11 MAR 2017 (photo © Lucas Rubio, iNaturalist observation 17573959, CC BY 4.0). **3-4**, Two views of a ♀ *Maevia inclemens* holding a captured robber fly by the prothorax, South Carolina. **5**, *Phidippus apacheanus* holding a captured robber fly, near Roswell, New Mexico, 27 AUG 2015 (photo © Jeff Cole, iNaturalist observation 22971123, CC BY-NC 4.0). **6-7**, Two views of a ♂ *Philaeus chrysops* holding a flesh fly, *Sarcophaga* sp., by the prothorax, Wiener Neustadt-Land, Österreich, 12 JUN 2023 (photos © Michael Knapp, iNaturalist observation 167085857, CC BY 4.0). **8-9**, Two views of a ♀ *Opisthoncus* holding a black soldier fly, (Stratiomyidae: *Hermetia illucens*), by the prothorax, New South Wales (photos © Jürgen C. Otto, used with permission).

Since many wasps prey on a variety of spiders (e.g., Finch 1997; Corey et al. 2021), one might expect that few spiders would attack them. However larger thomisids that wait for prey to arrive at flowers (e.g., *Misumena* and *Thomisus*) often capture large bees (Morse 1981; Huseynov 2007), and larger oxyopids often capture both bees and wasps (Figure 14.2; Turner 1979; Randall 1982; Nyfeller et al. 1987). Capture of larger wasps by salticids has not been frequently reported, but it does occur (Figure 14.3). More salticids appear to prey on odonates (Figure 15) and this should be relatively safe if the attacker can target the top of the head or prothorax, and avoid their spiny legs.



Figure 14. 1, ♀ *Lyssomanes viridis* holding a captured crane fly (Diptera: Tipulidae), South Carolina (photo CC BY 4.0, D. E. Hill). 2, ♀ *Peucetia viridans* holding a captured vespid wasp by the prothorax, South Carolina (photo CC BY 4.0, D. E. Hill). 3, ♀ *Phidippus mystaceus* holding a yellowjacket (Hymenoptera: Vespidae), Austin, Texas, 21 OCT 2017 (photo © Michelle Wong, iNaturalist observation 19347634, CC BY 4.0). These wasps are particularly abundant in the autumn when *P. mystaceus* mature.



Figure 15. Salticids with odonate prey. 1, ♀ *Colonus puerperus*, Maryland, 18 MAY 2019 (photo © Matt Muir, iNaturalist observation 25969276, CC BY 4.0). 2, *Hyllus semicupreus*, Bengaluru, 11 AUG 2022 (photo © Praveen T, iNaturalist observation 130403623, CC BY-NC 4.0). 3, ♀ *Colonus* cf. *sylvanus*, Valle del Cauca, Colombia, 18 AUG 2023 (photo © David Holland, iNaturalist observation 201489345, CC BY-NC 4.0).

Grasshoppers and katydids (Figure 16) have many dangerous features, including powerful mandibles, strong, spiny legs with a kick, and the release of noxious fluids. However they may represent an important food source for some larger salticids, including mature female *Phidippus clarus* (Figure 16.4-5).



Figure 16. Salticids with large orthopteran prey. **1-3**, ♀ *Phidippus carolinensis*, Fort Sill, Oklahoma, 1 JUL 2013 (photos © Victor W. Fazio III, iNaturalist observation 319941, CC BY-NC 4.0). **4-5**, ♀ *Phidippus clarus*, Oklahoma, AUG 2022 (photos © Thomas Shahan, iNaturalist observation 131406247, CC BY-NC 4.0). **6**, ♀ *Phidippus regius*, Frostproof, Florida, 11 NOV 2019 (photo by Daniel Estabrooks, iNaturalist observation 35588743, CC0). **7**, ♂ *Phiale guttata*, Guyane française, 14 JAN 2023 (photo © Elendil Cocchi, iNaturalist observation 147426678, CC BY-NC 4.0). **8**, ♀ *Phiale*, Bahia State, Brasil, 13 JAN 2022 (photo © Guilherme A. Fischer, iNaturalist observation 104916810, CC BY-NC 4.0). The male was mating with this female as she fed.

Large leaf-footed or squash bugs (Hemiptera: Coreidae) are herbivores and of little danger to a predator that stays away from their leg spines. However, they produce a series of noxious, volatile defensive secretions, including hexenal, hexanol, and hexylacetate (Prudic et al. 2008; Noge 2015). Larger salticids that can hold them at one end can limit contact as they wait for these secretions to dissipate (Figure 17.1-3). Cicadas (Hemiptera: Cicadidae) can vibrate powerfully (*stress sound* of ~110db; Smith & Langley 1978) when held by a predator, but otherwise have little defense against a targeted attack by a large salticid (Figure 17.4-5).



Figure 17. Salticids holding large hemipteran prey. **1-2**, ♀ *Phidippus putnami* holding a coreid, Bastrop County, Texas, 26 JUL 2019 (photo © Morgan Hay, iNaturalist observation 29609795, CC BY 4.0). **3**, *Phidippus* holding a coreid, Alamo Canyon, Arizona, 23 OCT 2021 (photo © Andrew Meeds, iNaturalist observation 104793228, CC BY 4.0). **4**, ♀ *Phidippus audax* holding a periodical cicada (*Magicicada*) by the prothorax, Alamo Canyon, Arizona, 23 OCT 2021 (photo © Andrew Meeds, iNaturalist observation 104793228, CC BY 4.0). **5**, Salticid holding the head of a cicada (*Guyalna*), Caacupé, Paraguay, 1 DEC 2017 (photo © Joaquín Movia, iNaturalist observation 53219065, CC BY-NC 4.0).

Adult Lepidoptera (Figure 18.1-3) have little protection from jumping spiders, other than the fact that capture by their wings is difficult. Some may delay or divert salticid attacks by mimicking either a salticid face (Hill et al. 2019; Hill 2022; Tripathy & Singh 2024) or an insect head (Hill 2018b) at the rear of each hindwing (Sourakov 2013; Hill 2018b). Larvae (Figure 18.4-6) are soft-bodied, but need to be attacked by the top or rear of the head as they can twist around and have both claws and strong mandibles.

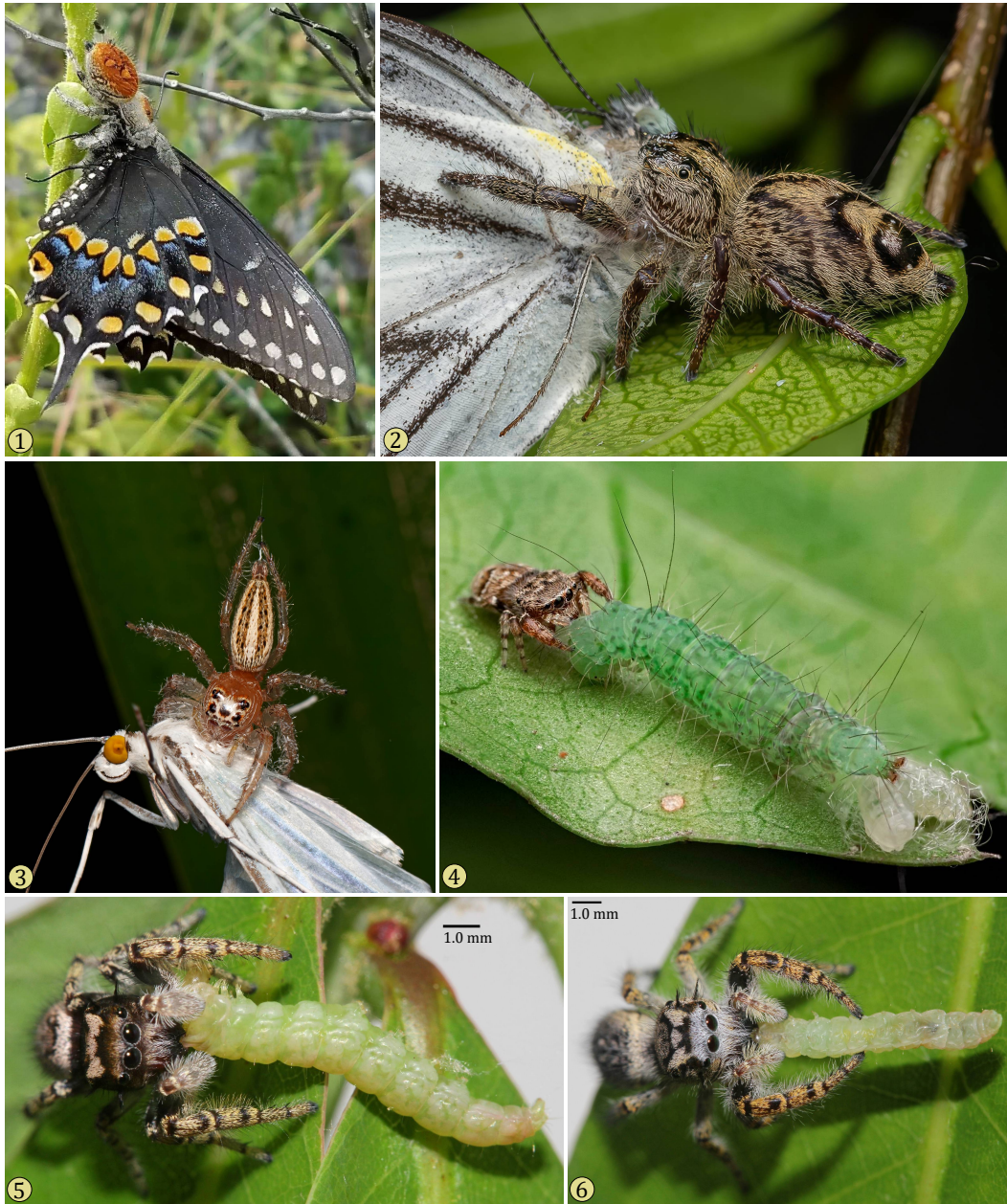


Figure 18. Salticids with lepidopteran prey. **1**, ♀ *Phidippus regius* holding a papilioniid, Osceola County, Florida, 16 OCT 2019 (photo © Ray Simpson, iNaturalist observation 34675101, CC BY-NC 4.0). **2**, ♀ *Hyllus diardi* holding a butterfly, Penang, Malaysia, 1 JUN 2016 (photo © Roman Prokhorov, iNaturalist observation 147315153, CC BY-NC 4.0). **3**, ♀ *Colonus* cf. *sylvanus* holding a moth, Quintana Roo, México, 24 JUL 2022 (photo © Luis Fernando Valdez Ojeda, iNaturalist observation 127769069, CC BY 4.0). **4**, *Rhene* feeding on a caterpillar, Bengaluru, Karnataka, 25 DEC 2020 (photo © Girish Gowda, iNaturalist observation 104477791, CC BY-NC 4.0). **5-6**, Penultimate ♂ (**5**) and ♀ (**6**) *P. mystaceus* from Seminole County, Oklahoma, feeding on small caterpillars (CC BY 4.0, D. E. Hill).

Recently it has been reported that larger salticids such as *Phidippus regius* prey on vertebrates, to include tree frogs (Hylidae; Figure 19.1-2), small lizards (*Anolis*), and even the young of altricial birds (Ahmed et al. 2017; Nyffeler et al. 2017b, 2021). Given the size of the insects that these spiders pursue, this is not unexpected. Attack to the top of the head, and avoidance of the kicking legs, of a small tree frog is similar to an attack on a large grasshopper. Predation on vertebrates by other spiders (e.g., *Dolomedes*, Figure 19.3-4; Bleckmann & Lotz 1987) is well known. *Dolomedes* also take very large insects (Figure 19.5).



Figure 19. Spiders that feed on vertebrates. **1**, ♂ *Phidippus regius* feeding on a tree frog, near Tampa, Florida, 23 SEP 2018 (photo © Ellen, iNaturalist observation 18096717, CC BY-NC 4.0). **2**, ♂ *Phidippus regius* feeding on a tree frog, Orange County, Florida, 16 SEP 2022 (photo © Ernst Weiher, iNaturalist observation 135282328, CC BY-NC 4.0). **3**, ♀ *Dolomedes scriptus* feeding on a fish, Nipissing District, Ontario, Canada, 21 JUN 2015 (photo © juliederocche, iNaturalist observation 35746437, CC BY-NC 4.0). **4**, ♀ *D. triton* feeding on a fish, Palm Beach County, Florida, 14 MAR 2023 (photo © bleidig, iNaturalist observation 157095030, CC BY-NC 4.0). **5**, Penultimate ♂ *Dolomedes* holding a large dragonfly (*Aeschna cyanea*) by the prothorax, Kraftshofer Forst, Deutschland, 15 OCT 2000 (photo © Hans Böckler, iNaturalist observation 87032215, CC BY-NC 4.0). Compared to this insect, small fish appear to be easier prey. However *Dolomedes* must capture their fish in the water.

Discussion

The ability to capture prey at a distance with a jump has given salticids a particular advantage over many other arthropods and even small vertebrates. As shown here, even larger and more powerful prey can be captured successfully *as long as the soft-bodied salticid can avoid grappling with that prey*. This requires special skills and equipment, most notably 1) the ability to evaluate and target specific prey, and specific parts of that prey's anatomy, 2) the ability to execute a jumping attack that is both accurate and precise, and 3) the ability to overcome that prey with venom.

Targeting. Several laboratory studies (e.g., Jackson & Wilcox 1990; Edwards & Jackson 1993, 1994; Bartos 2000) have demonstrated that salticids use a different approach to capture different kinds of prey. Choice experiments conducted in the laboratory (e.g., Roach 1987; Nelson & Jackson 2006, 2009, 2012) also support the view that salticids are selective. Individual spiders of the same species may vary in their aggressiveness or response to prey (Chang et al. 2017; Powell & Taylor 2020). Learning of predatory skills by salticids has not been found (Edwards & Jackson 1994), but salticids appear to avoid chemically defended prey in the short-term after contact (Hill 2016). It is also important to note that locally abundant prey may be selected more often in nature (*density-dependency*; see Kinney et al. 2023).

Accuracy and precision of the attack. Accurate execution of a predatory jump requires detailed computations that include, as input, the relative alignment of the surface supporting the predator, the position and alignment of each leg, the distance of the prey, the direction of the prey relative to gravity, and the position on the prey that is to be attacked (Hill 2010a, 2010b, Hill et al. 2021). The *Phidippus audax* shown in Figure 11.1 had just jumped ~10 cm down *from an upside-down position* to capture a large lycosid by the carapace. Direction relative to gravity determines the range that is possible for a jump, and salticids appear to only attempt *possible* jumps toward prey. Salticids jump at a variable take-off velocity and elevation relative to the prey direction to reach that prey. This control is even more important when that prey is dangerous. In addition, because the attack itself is very fast, the distance at which the attacking salticid brakes on the dragline, thereby pulling prey away from a surface by elastic rebound, must be determined *before* the execution of a predatory jump. The ability of a salticid to jump with both accuracy (*on target*) and precision (*repeatable performance*) is most important for its success as a predator, far more than the horizontal range of those jumps, something that is greatly exceeded by many insects that lack their accuracy.

Venom. Although many detailed studies of spider venom have been published (Quistad et al. 1992; Schwartz et al. 2012; Langenegger et al. 2019), few have considered the Salticidae. Each spider venom that has been studied contains a mixture of various cytotoxins and neurotoxins. However, one study of the effect of arthropod venom taken from 30 different species (including 26 species of spiders) on both insect and mammalian tissues found that:

The most cytotoxic venoms to the four cell lines were from predatory jumping spiders (Salticidae, *Phidippus* sp.) and a centipede (*Scolopendra* sp.), with concentrations for 50% response of 1–8 µg venom per ml. The cytotoxicity of *Phidippus ardens* venom at these levels was instantaneous and evidenced by dramatic disruption of cell membranes resulting in cell collapse. (quote from Cohen & Quistad 1998)

In other words, some large salticids have extremely potent venom. Russell (1970) reported the painful bites of a *Phidippus formosus* (= *P. johnsoni*) on the top of a hand, associated with a 4 cm wheal and both itching, pain and swelling of the hand that lasted for at least 9 days (even after treatment with methdilazine), with evidence of local tissue damage (*lesions*) visible for at least 2 weeks. My own experience with the bite of a *P. mimicus* was somewhat similar, but more localized (see Hill et al. 2021, fig. 7). We should expect to find considerable variation in both toxicity and composition of salticid venom when comparative studies are available.

Age of the attacking salticid. Salticids of different ages have different capabilities, and they are known to target different prey (Edwards & Jackson 1994; Bartos & Szczepko 2012). They also have different enemies. Whereas a young *Colonus sylvanus* is easy prey for an adult *Lyssomanes viridis*, adult *C. sylvanus* frequently prey on even adult *L. viridis* (Figure 12.1-3). In studies of spider ecology, and spider impact on local ecosystems, the changing diet of immatures is all-too-often overlooked.

Considerations of risk and reward. Attempts to prey on large and dangerous prey are not always successful, and may be fatal. For salticids to engage in this risky behavior, the reward must be commensurate. Any time that a salticid ventures from its retreat to forage, risk is most certainly increased. Thus the ability to secure a great deal of food from a single capture can be associated with a reduction in foraging risk. For example, female *Phidippus clarus* (Figure 16.4-5) mature at the end of summer, when large grasshoppers are also maturing in numbers, and are usually abundant, in their prairie or old field habitat. A single capture of just one grasshopper might allow a female *P. clarus* to remain in her shelter and rear a relatively large brood without having to emerge.

Specialists or opportunists? Many salticids are thought to be specialists on spiders (*araneophagous*), ants (*myrmecophagous*) or even mosquitoes (*culiciphagous?*). However it is important to recognize that we have little knowledge of morphological changes associated with these kinds of specialization in salticids, apart from the presence of thin metatarsi and tarsi in some salticids (e.g. *Portia*), apparently facilitating their movement on silk lines. Local diet specialization (e.g., synanthropic *Plexippus paykulli* feeding exclusively on the German cockroach, *Blatella germanica*; Nyffeler et al. 1990) may be associated more with opportunity (or a *facultative response* to prey density) than with preference.

Problems with the study of diet. Although there are many published studies pertaining to the diet of spiders, it is really difficult to obtain reliable quantitative information in this area. Collected observations in the field or laboratory (or *anecdotes*, e.g., Bilsing 1920; Jackson 1977; Edwards 1980; Bartos 2004; Guseinov 2005; this paper) are useful indicators of what a spider *has done*, and *might do*, in the field, but they do not tell us what is actually happening out there, and give little indication of the relative frequency of these events. Even attempts at sampling at regular or random intervals (e.g., Young 1989; Schadeegg & King 2021) are prone to a number of sampling errors. What you see may be greatly impacted by *where* you look, *when* you look, weather, other local conditions (that may change with time), population densities, your vision, and your bias. It is well known that we tend to see what we are looking for (Wolfe 2020). Even assuming that all of the nuances of sampling could be worked out, variations in the handling of different prey can effect results. For example, with some prey, spiders may tend to move to a concealed position. Even assuming that all feeding spiders are equally visible, you still have to consider the fact that the time required to feed will vary by prey type. Consider the following example:

prey type	captures in area	time to feed/capture	total time feeding
A	100	10 minutes	1000 minutes
B	50	30 minutes	1500 minutes
C	25	80 minutes	2000 minutes

Since all feeding spiders are equally visible, the most frequent event that you will tally is predation on (C), when in fact predation on (A) occurs four times as frequently. Nuances like this should be recognized and taken into account in a field study of predation, but they seldom are. Direct observation of (or *following*) single spiders might give you a better measurement of predation in the field, but unfortunately this is very difficult and time-consuming, particularly since salticids are easily distracted by a human observer (the *observer effect*). But you should still get some insight from this approach. Anecdotes are informative.

The published results of prey choice experiments in the laboratory (e.g., Roach 1987; Huseynov et al. 2005; Nelson & Jackson 2006, 2009, 2012), particularly those using immobile prey, are difficult to interpret. How often do spiders in the field deal with a similar series of choices? In addition, microenvironmental conditions in the field (e.g. wind, solar radiation, temperature, illumination, time of day, movement in the surroundings) can change from moment to moment, quite different from a laboratory setting. The demonstration that some salticids can survive in the laboratory by scavenging (Vickers et al. 2014) clearly represents a capability, but this may have little relevance with respect to their diet in a natural environment.

Particularly since entomologists tend to be concerned with insect control, spider predation has received attention in the past. Even without this concern, the predatory behavior of spiders poses many interesting and challenging questions related to selectivity, risk/reward, response to resource and microclimate fluctuations, competition, and behavioral genetics.

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