

Notes on the jumping spiders *Colonus puerperus* (Hentz 1846) and *Colonus sylvanus* (Hentz 1846) in the southeastern United States (Araneae: Salticidae: Amycoidea: Gophoini)¹

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Introduction

The two species of *Colonus* (*Colonus* F. O. Pickard-Cambridge 1901, formerly placed in *Thiodina* Simon 1900) that are commonly found in the southeastern United States are very similar to each other in most respects and have often been confused. Here I will follow the classification of Richman & Vetter (2004), whose review included descriptions that separate the two species, *C. puerperus* (Hentz 1846) and *C. sylvanus* (Hentz 1846). Hentz' description of the female *Attus puerperus* (page 360, plate XXI, figure 22) is actually a better fit for the female of *C. sylvanus*: *abdomen with about twelve black dots, underneath with a black spot near the apex*. Hentz' drawing of a male *A. sylvanus* (page 364, plate XXII, figure 10) also clearly depicts the isolated rectangular, middorsal patch of carapacial scales that distinguishes the male *C. sylvanus*. The Peckhams first (1888) recognized the male *A. sylvanus* Hentz 1846 as a synonym of the female *A. puerperus* Hentz 1846, and moved this species into the genus *Plexippus*. However some 21 years later (1909) they changed the name of *P. puerperus* to *T. sylvana*, and applied the name *T. puerpera* to a different species, attributing both species names to Hentz under Simon's genus *Thiodina*. *T. puerpera* (now *C. puerperus*) might be more accurately attributed to the Peckhams as we have no evidence that Hentz ever described this species. The Peckhams could find little to separate their female *T. puerpera* from *T. sylvana*. In fact, there are quite a few differences between the two. For more than 100 years the naming of the two species followed Peckham & Peckham (1909). Recently they were both transferred to *Colonus*, with *C. sylvanus* designated as the type species for that genus (Bustamante et al. 2015).

It is unfortunate that two reviews or revisions that include species of *Colonus* not found within the borders of the United States exist only in the form of unpublished dissertations (Wolff 1985; Nogueira 2003). About 14 species of living *Colonus* have been described to date, mostly from South America (11 species). At least 3 species are widely distributed in Central America, the Caribbean, and the southern nearctic region including Mexico and the United States (Figure 1; Nogueira 2003; Richman & Vetter 2004; WSC 2018). In addition, one extinct species of *Colonus* has been described from Miocene Dominican amber (Wolff 1985, 1990; 15-20 Ma age based on Iturralde-Vinent & MacPhee 1996). The three nearctic species include *C. puerperus* and *C. sylvanus*, both reported from the southeastern United States, but perhaps also found as far south as Panama (Nogueira 2003), and *C. hesperus* (Richman & Vetter 2004), ranging from the southwestern United States to southern Mexico (Richman et al. 2012). It is thus reasonable to describe *Colonus* as an essentially neotropical genus, with only a few species ranging into warmer parts of nearctic North America south of the 10°C isotherm.

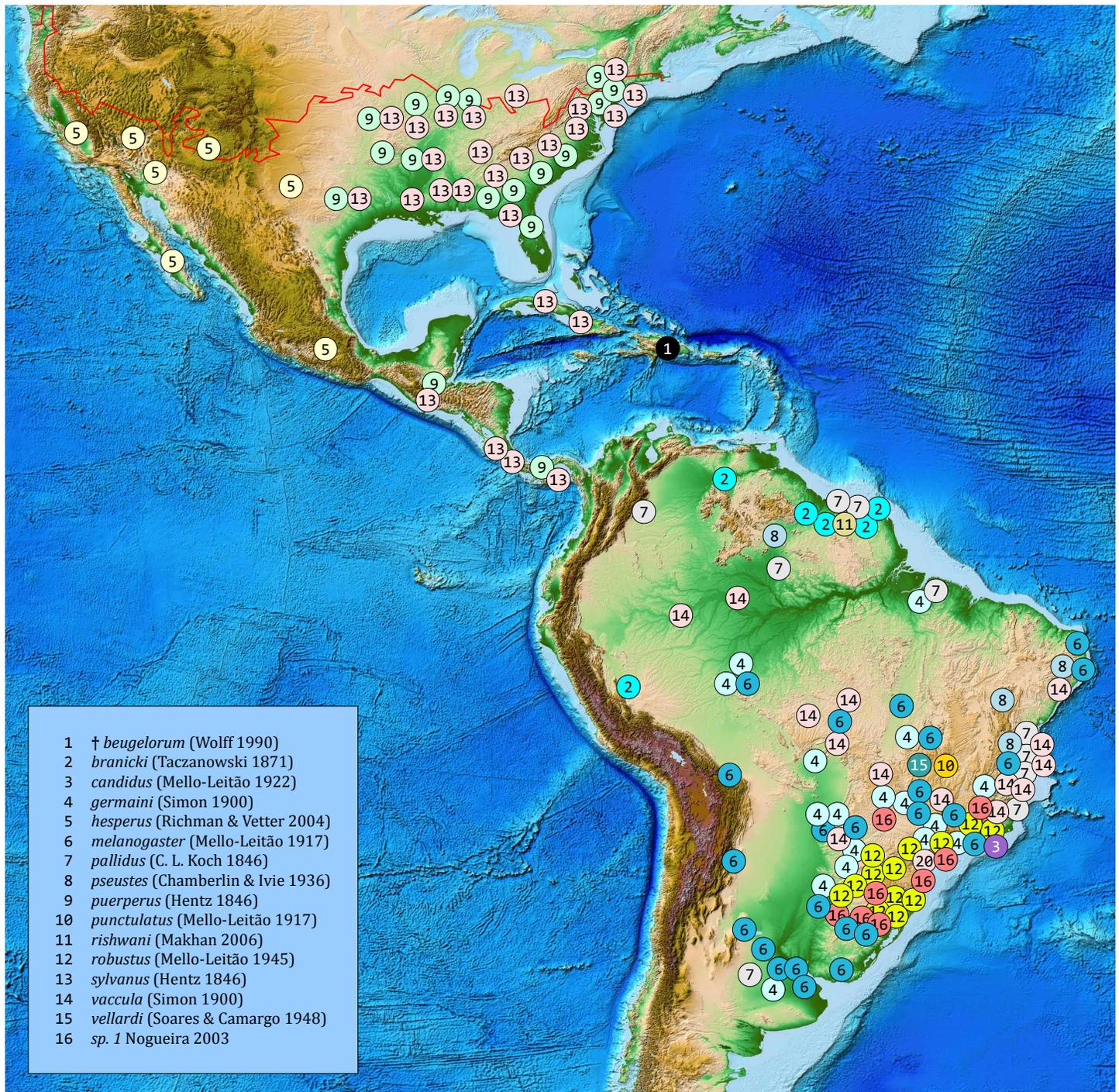


Figure 1. Distribution of known *Colonus* species. In addition to locality data associated with published descriptions which often only identify the country of origin, locality records presented by Nogueira (2003) and Richman *et al.* (2012) have also been used to produce this view. With a Miocene (15-20 Ma; Iturralde-Vinent and MacPhee 1996) representative from the Dominican Amber (1; Wolff 1985), *Colonus* was apparently able to move out of South America into the Caribbean long before the formation of the Central American Land Bridge. Although both *C. puerperus* (9) and *C. sylvanus* (13) have been reported from Central America as shown here (Nogueira 2003; Arias 2005), these records need additional confirmation. Most collecting of *Colonus* has been associated with either southern Brazil or the southern United States, and our knowledge of this widely distributed genus outside of these two areas is quite limited. The North American species are generally found south of the 10°C isotherm based on mean annual air temperature (red line on map; climate data from Owenby *et al.* 2009). Background data and imaging courtesy of NOAA Satellite and Information Service (Amante & Eakins 2009).

Some of the Brazilian *Colonus* (Figure 2) are surprisingly similar to the nearctic *C. sylvanus* and *C. puerperus*, particularly in light of the fact that this appears to be an ancient genus.



Figure 2. *Colonus* sp. from Maria Paula, Niteroi, Rio de Janeiro, Brazil (August 2011). **1**, This immature or female *Colonus* could easily be mistaken for the North American *C. puerperus*. **2-4**, Three views of an adult male *Colonus* sp., distinct but similar to both *C. puerperus* and *C. sylvanus*. Photographs Copyright © Maxwel Rocha, used with permission.

There are few published accounts dealing with the biology of *Colonus*. This genus has long been distinguished by the presence of two pairs of bulbous setae (or *bulbosae*), of unknown function, proximal to two pairs of macrosetae (spines) on the underside of tibia I. These are present in animals of both sexes and all ages (Comstock 1913; Richman & Vetter 2004; Kaldari 2009). Carroll (1977) described the unusual nocturnal behavior of a *Colonus* (almost certainly *C. hesperus*) in California: *they hang upside down for the entire night by a length of dragline several inches long, which is securely anchored to the foliage*. Although I have observed some southeastern *Colonus* to suspend themselves in this manner for several minutes, particularly when feeding, I have not seen them doing this at night. The higher, indeed often *torrential*, rainfall in the southeastern United States suggests that more of a shelter would be needed here.

As I have observed *Colonus* in the southeastern United States over a number of years, I have always been impressed with their slow and deliberate movements, as well as their ability to detect and to stealthfully stalk immobile prey, including other spiders. Unlike many salticids, they do not flicker their pedipalps, either to advertise their presence, or to interact with their prey. They can move quickly if alarmed, but their normally slow movement supports close observation of behaviors, including the extension and retraction of claws and footpads, that are usually difficult to see in other salticids. I have documented some of this behavior in a series of videos (*C. sylvanus*; Hill 2007a-d), that should be downloaded for viewing in their highest resolution. Here I will focus on more recent studies of the prairie species *C.*

puerperus and the woodland *C. sylvanus*, highlighting not only the similarities of the two species, but also some differences that may be correlated with their habitat separation.

Relationship to other salticids

Recognized as a salticine, *Colonus* and its close relatives (Gophoini) represent a distinctive group within the Amycoidea, a clade that is basal within the large salticine clade relative to the much larger salticoid clade (Figure 3; Maddison and Hedin 2003; Maddison et al. 2008; Maddison 2015).

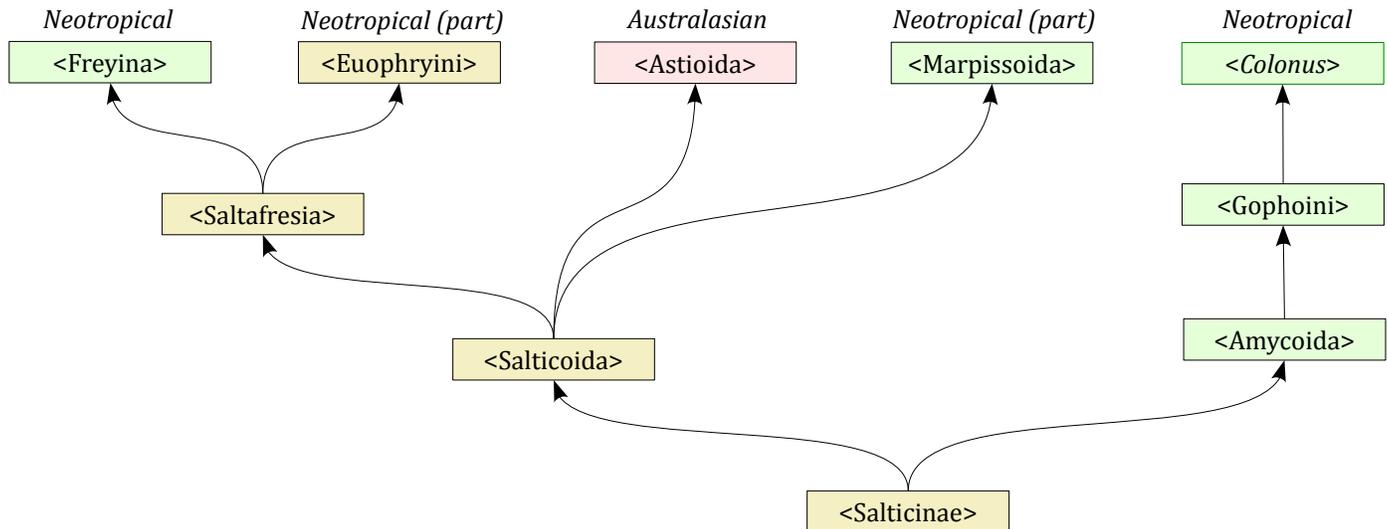


Figure 3. Simplified view depicting the hypothetical phylogenetic relationship of *Colonus* to other salticine jumping spiders. Each box represents an ancestral species, each corresponding to a clade, not all of which are named or placed here. Colors reflect the major continental distribution of each clade, and all major Neotropical clades are represented. The Neotropical Amycoidea are basal with respect to the more diverse salticoids. Some data also supports the hypothesis that the Gophoini (formerly Thiodininae) are basal with respect to the other amycoids (Bodner & Maddison 2009).

Habitat

Although they occupy the same geographic range, *C. puerperus* is primarily a tallgrass prairie species, commonly found in dense grasses and on associated herbaceous plants, and *C. sylvanus* is known as an inhabitant of shrubs in the woodland understory or along a woodland margin (Richman & Vetter 2004; Edwards & Hill 2008). The behavioral correlates of this habitat separation are little known. I have consistently observed this separation in areas ranging from northern South Carolina to central Georgia. In some cases, I have found *C. puerperus* on grasses only a few meters away from woodland shrubs occupied by *C. sylvanus*. Richman & Vetter (2004) reported the presence of adults of both species in almost every month of the year, except for January. In the northern part of South Carolina, I have usually found *C. puerperus* maturing from September to April, and *C. sylvanus* maturing somewhat later, from April into the early summer. Between April and August, the adult males of *C. puerperus* are very hard to find here. Both species can be locally abundant. The challenge in finding good populations of *C. puerperus* lies in its native tallgrass prairie habitat (Figure 4), one that scarcely exists in its original form. Old field (limited cultivation for many years) or ruderal (roadside or disturbed ground) areas can only support prairie species in the southeast if they are subject to a program of mowing, which controls their otherwise rapid succession to forest. If they are mowed too frequently (for example, every year) or in the summer they appear to lose their plant biodiversity and their *C. puerperus* populations. The woodland habitats favored by *C. sylvanus* are the natural product of succession in the southeastern United States, and may be viewed as a more permanent resource. In South Carolina, forests have lost much of their

diversity with respect to the smaller native plant species that live in clearings and under the canopy, but the broadleaf trees themselves require no special maintenance once they are established (Porcher & Rayner 2001).



Figure 4. Typical *Colonus* habitats in Greenville County, South Carolina. **1**, Grassy, ruderal or old field habitat (foreground) populated with *C. puerperus*. This field included a mixture of tall grass and herbaceous species, and *C. puerperus* were active on both during daylight hours. Margins and understory of the hardwood forest in the background were populated by *C. sylvanus*. **2**, Detail of dry grasses from (1). Sweeping these tall grass clumps led to the capture of most *C. puerperus*, and they may have found shelter in the dense thatch of these clumps. **3**, Inhabited molting sac of an immature *C. puerperus*, from a *Rubus* growing in the open field shown in (1). **4**, Detail of sunny forest margin shown in (1), where shrubs and herbaceous plants were inhabited by *C. sylvanus*.

In an effort to determine their resting sites, I followed two adult male *C. sylvanus* in the evening. Both concealed themselves under fallen leaves on the forest floor. It is possible that both *C. sylvanus* and *C. puerperus* frequently shelter in dry plant material near the ground, but I have few observations to support this. As shown in Figure 4:3, *Colonus* can seal off the underside of curved leaves with a silk barrier in the shape of a flat or paraboloid surface, to construct their molting sacs. These appear to be tightly sealed and parchment-like, without the multiple entrances and more complex layering of silk associated with the resting/molting sac of a dendryphantine like *Phidippus*. *C. sylvanus* were often observed upon or under leaves 1-2 m above the forest floor, and in these locations I have been able to find both males and females during the day.

Identification of adult spiders

A series of adult *Colonus puerperus* and *C. sylvanus* are depicted in Figures 5-8 to illustrate distinguishing field marks and some of the variability found in each species.



Figure 5. Representative adult male *Colonus puerperus* from Greenville and Laurens Counties, South Carolina. The posteromedian tract of white scales (6, arrow) and the lack of red scales around the margins of the ocular quadrangle distinguish *C. puerperus* males. When present, the red to orange area of the dorso-anterior carapace of *T. puerpera* is associated with the cuticle, not with red scales as in *T. sylvana*. Each scale bar = 1.0 mm.



Figure 6. Representative adult male *Colonus sylvanus* from Greenville County, South Carolina. Often these males have multiple longitudinal tracts of white scales below the PLE (3, arrow), but the most distinguishing features are the isolated rectangular patch of white scales between the PLE (9, arrow), the lack of a posteromedian line of white scales behind this patch as in *T. puerpera*, and the presence of scattered red scales around the eyes. As with *C. puerperus*, the darkness of adult male pigmentation varies greatly in *C. sylvanus*. The spider shown in (2) had only a very small group of white scales between the PLE when it matured, but the bright red scales around the eyes mark it as a *T. sylvana*. Unless otherwise indicated, each scale bar in this and in subsequent figures equals 1.0 mm.



Figure 7. Representative adult female *Colonus puerperus* from Greenville and Laurens Counties, South Carolina, showing some of their variation in size and coloration. Distinctive field marks of this species include the presence of white to ivory scales in the mid-lateral bands of the dorsal opisthosoma (3, arrow), the translucent yellow coloration of the prosoma and legs (visible even when standing on a white background), the clear coloration of the lateral and posterior carapace (not flecked), and the lack of red scales around the eyes. Opisthosomal stripes were sometimes lacking or obscure, as shown in (5).



Figure 8. Representative adult female *Colonus sylvanus* from Greenville County, South Carolina. These can be identified by the grey to red-brown band (3, arrow) between the mid-lateral opisthosomal stripes, the presence of orange to red scales around the eyes, and the presence of dark flecks in the otherwise clear parts of the carapace lateral and posterior to the ocular quadrangle. This species is translucent, but lacks the deeper yellow coloration of *C. puerperus*. However, because this spider assumes more of the color of its background than does *C. puerperus*, it may also appear to have a yellowish cast.

As noted in the introduction, Hentz' (1846) description of the female *Attus puerperus* is actually a better fit with *Colonus sylvanus* than with *C. puerperus*. As shown in Figures 7 and 8, both species have an abdomen with about twelve black dots (or at least the number and placement of black spots on the dorsal opisthosoma is about the same in both species), but it is *C. sylvanus*, and not *C. puerperus*, that has the prominent black spot near the apex on the ventral opisthosoma (Figure 9). The epigyna of the two species are also quite different; that of *C. sylvanus* is much larger and darker (Figure 10).

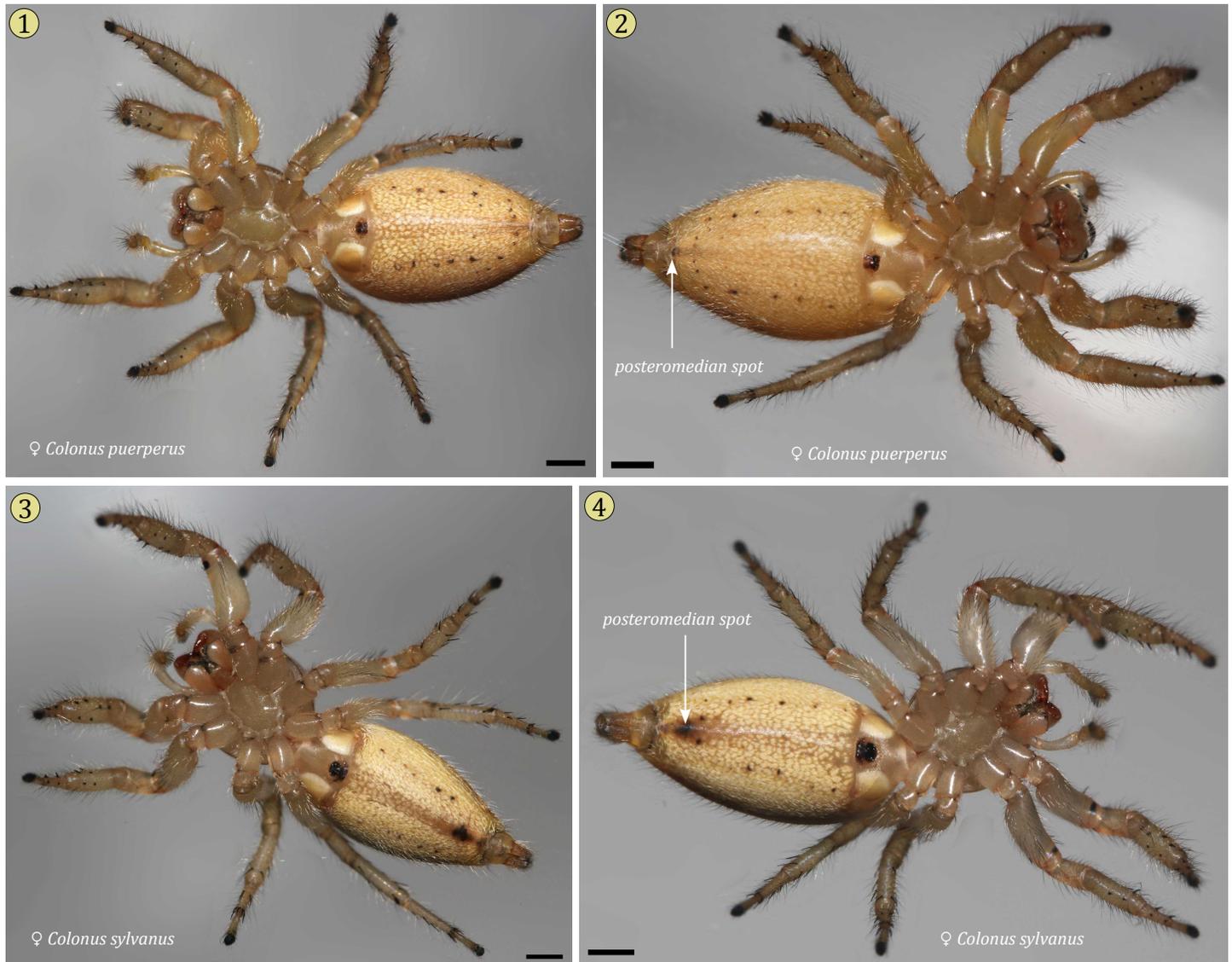


Figure 9. Ventral views of adult female *C. puerperus* (1-2) compared with *C. sylvanus* (3-4), against a white background. A small and indistinct postero-medial spot (2, arrow) may be seen on the ventral opisthosoma of some *C. puerperus* females, but a large and prominent dark spot in this position is a characteristic of *C. sylvanus* (4, arrow). Other notable differences include the yellowish translucent coloration of *C. puerperus*, and the much larger, darker epigynum of *C. sylvanus*.

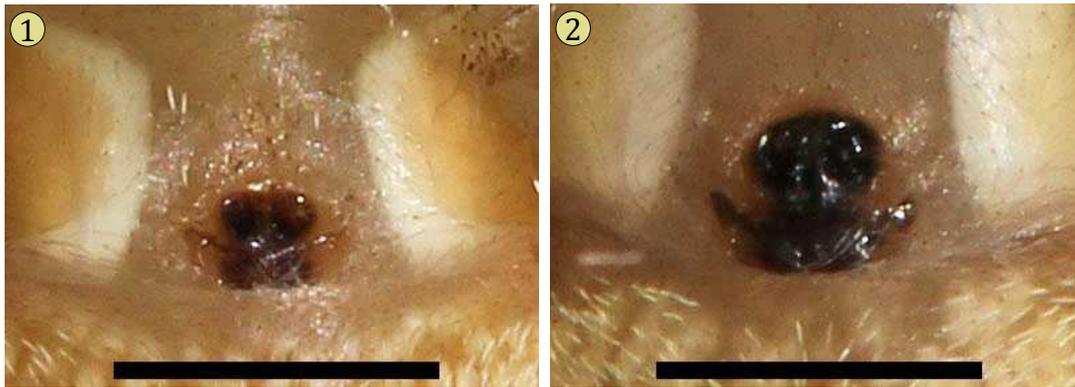


Figure 10. Detailed ventral views of epigyna of living *C. puerperus* (1) and *C. sylvanus* (2), from two spiders of similar size. The epigynum of *C. sylvanus* is much larger and darker.

Contests between males

I first observed a contest between two male *Colonus sylvanus* on the upper leaves of a shrub growing in full sunlight along a forest margin. I did not have a camera at the time, but was able to capture the two combatting males and brought them indoors with part of that shrub, where they resumed their combat. Other photographs of male-male contests shown here were also based on spiders placed on plants indoors, under artificial lights.

In *C. puerperus*, males that sight other males at a distance first square off by raising the body, moving the pedipalps laterally to expose the chelicerae, and turning the opisthosoma to one side or the other (Figures 11-12). I have observed a similar display in many other salticids, including *Phidippus* and *Platycryptus*.



Figure 11. Photomontage showing three successive positions (1-3) of two male *Colonus puerperus* as they displayed to each other at a distance. Both males maintained an erect stance as they faced the other and stepped from side to side during this encounter. Note the wide separation of the pedipalps to reveal the darkly iridescent and flattened chelicerae, and the orientation of the opisthosoma, down and to the side. The following conventions apply to this and to subsequent figures depicting either two spiders or the interaction of a spider with its prey at a distance: Images with the same number represent simultaneous positions taken from the same photograph, and the sequence of these numbers in a photomontage represents the actual sequence of the positions that are shown.

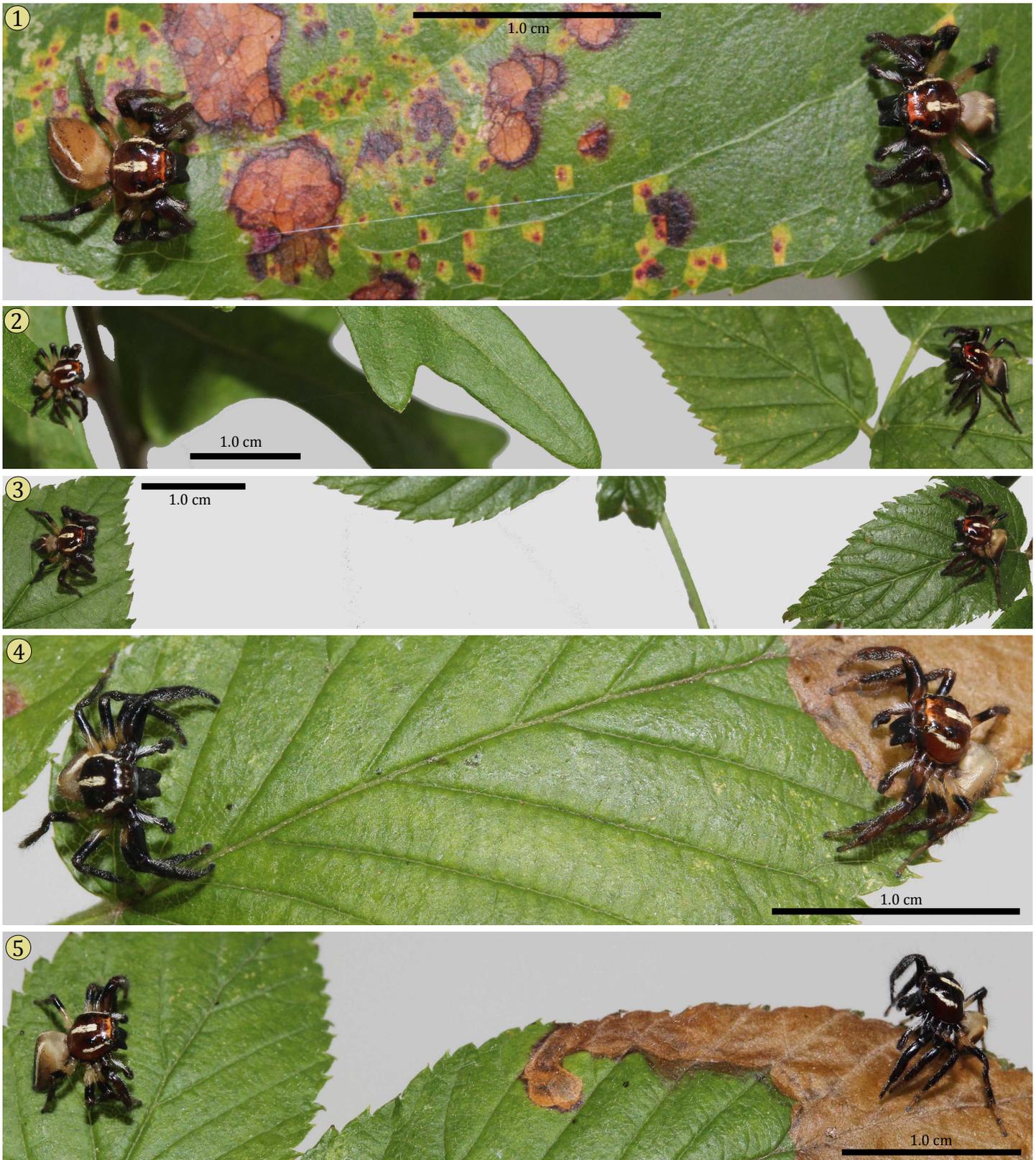


Figure 12. Images from five separate encounters, showing male *Colonus puerperus* displaying at a distance.

During these encounters, male *C. puerperus* would move from side to side, and then approach each other. If one of the spiders did not flee, a distinctive display with legs I and II extended laterally was usually observed when the spiders were in proximity (Figure 13). This often led to violent grappling or striking with legs I and II as the spiders came into contact, with the flat surfaces of the chelicerae close to each other, a struggle that was rapidly resolved with the flight of one of the combatants.



Figure 13. Images from two sequences (1-2, 3-4) where male *C. puerperus* approached each other during an encounter. The lateral extension of legs I and II was apparently a threat display, as it often led to violent grappling between the males.

The male-male contests of *C. sylvanus* that I have observed, including one in a natural setting, involved the same two components of *display at a distance*, followed by approach by both combatants (unless one fled) and *combat*. The initial display position (Figures 14-15) was similar to that of *C. puerperus*, but *C. sylvanus* males did not extend legs I and II in a threat position as they approached each other. Instead, they moved into a position of direct contact with the chelicerae, with legs I (only) extended, apparently careful not to hit each other with these legs (Figures 16-17). Combat then consisted of a formal *pushing contest* with the flat front surfaces of the chelicerae in contact, until one male gave way and fled. It is likely that the texture of the anterior cheliceral surfaces, consisting of horizontal grooves, allowed the males to directly engage or interlock their chelicerae during these contests.



Figure 14. Positions assumed by male *C. sylvanus* as each displayed to another male at a distance. In all respects these displays at a distance compared with those of *C. puerperus*.



Figure 15. Montage of two successive images (1-2) showing the interaction of two male *C. sylvanus* at a distance. The spider at left moved little between the two images, as the spider at right stepped to the side. In position (2), both spiders positioned at least one leg at the edge of the leaf, a position that facilitates rapid escape by flipping to the opposite side of the leaf. This can be viewed as a threat with a *fall-back position to retreat if necessary*.

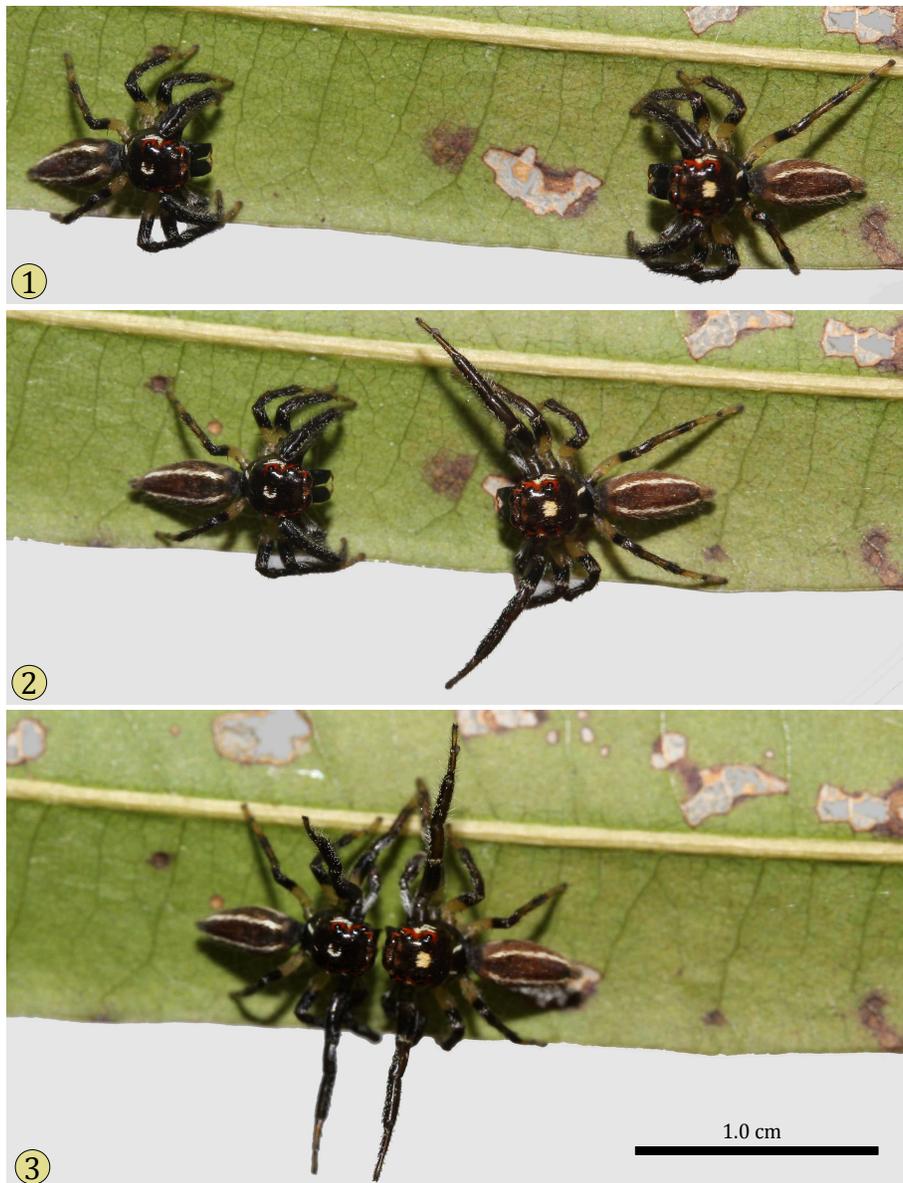


Figure 16. Sequence of images (1-3) showing the approach of two *C. sylvanus* males to engage in a pushing contest with legs I outstretched.

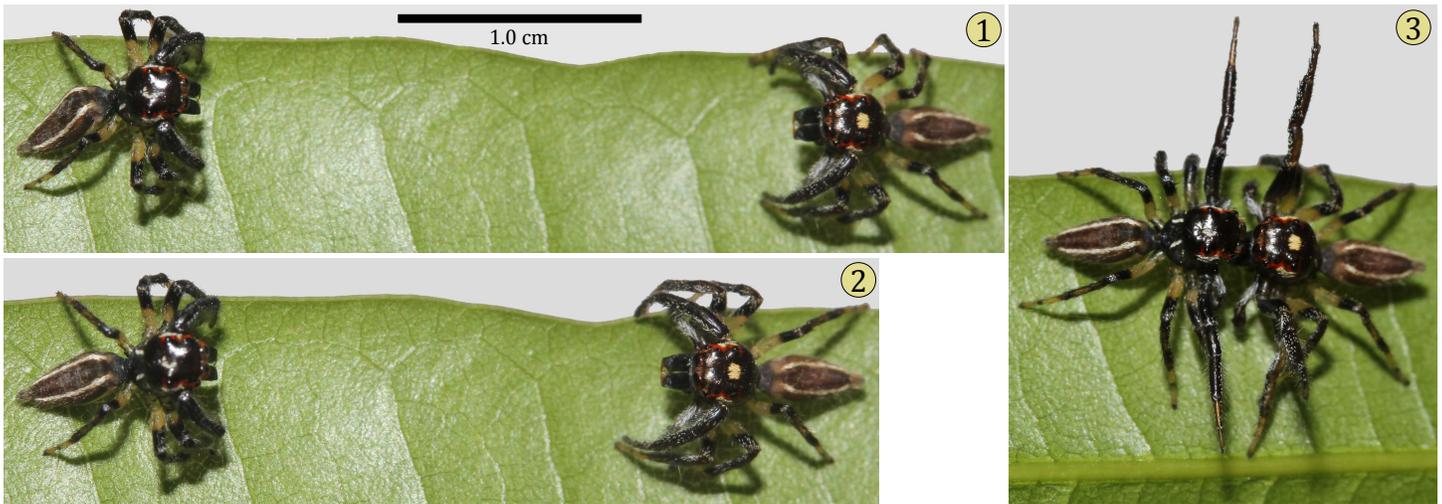


Figure 17. A second sequence of images (1-3) showing the approach of two male *C. sylvanus* to engage in a pushing contest with legs I outstretched, and the flat anterior surfaces of the chelicerae in direct contact.

I consistently observed these differences in the male-male encounters of the two species, but of course it is possible that with different individuals, or in different populations, variations might be observed. The formal (*ritual* or *polite*) contests of *C. sylvanus* males seemed to be more of a direct and orderly measurement of relative strength, carefully avoiding the possibility of inflicting damage with the macrosetae of legs I by keeping these legs out of the action. In contrast, the many close encounters of *C. puerperus* males that I have observed appeared to be much more dangerous to the combatants, with the macrosetae of legs I and II used to directly and quickly attack the opponent, in a kind of *attack frenzy*. In a recent study (Otto & Hill 2012) we found that *Maratus vespertilio* males also struck at each other with legs I and II in close combat, but these interactions were prolonged, formal engagements in which each combatant hopped at or struck the other in turn.

Partly to consider agonistic behavior as one factor in the isolation of these related species, I twice placed size-matched males of the two species together on a plant. Each time, the two males displayed to each other at a distance, and then both approached the other. In both cases, as soon as the *C. puerperus* male assumed its four-legged (legs I and II) threat position (Figure 13:2,4), the *C. sylvanus* male fled from the contest. This supports the idea that this particular threat position does not play a role in the contests of male *C. sylvanus*.

Courtship and mating

All of my observations of courtship and mating by *Colonus* are based on males and females placed on plants indoors, under artificial lighting. As shown in Figure 18, the display of a male *C. puerperus* that has sighted a female at a distance is similar to that of many other salticids (see Richman 1981 for references). The male faces the female and raises and extends legs I laterally, often turning the opisthosoma down and to the side. The zig-zag approach of a male to a sighted female (Figure 19) has been observed in many other salticids. In *Colonus*, I have only observed this movement on leaf surfaces where it was possible, and in these cases the male would move from side to side until the female stopped turning to face it, and would then advance and attempt to touch and mount the female. Thus it appears that this side to side movement is a test of whether the female is safe to approach. In *Colonus*, as in some *Phidippus*, I have not observed any complex and detailed evaluation of male performance by a female, as has been observed in the *Habronattus coecatus* group (Elias et al. 2012). The reason for elaborate rather than simple courtship is the subject of much speculation. In the case of *Colonus* and many other salticids, it may be that just *getting to the female first* is such an important measure of fitness that a female that was more selective for ornamental details and behavioral nuances would not be picking the best mate.



Figure 18. Courtship display by two male *C. puerperus* (1, 2-3) that have sighted a female. This differs from the four-legged threat display of *C. puerperus* (in male-male encounters) in that the pedipalps are not widely separated, and only legs I are raised above the surface. In *C. puerperus*, the length of the extended leg I is close to the body length.

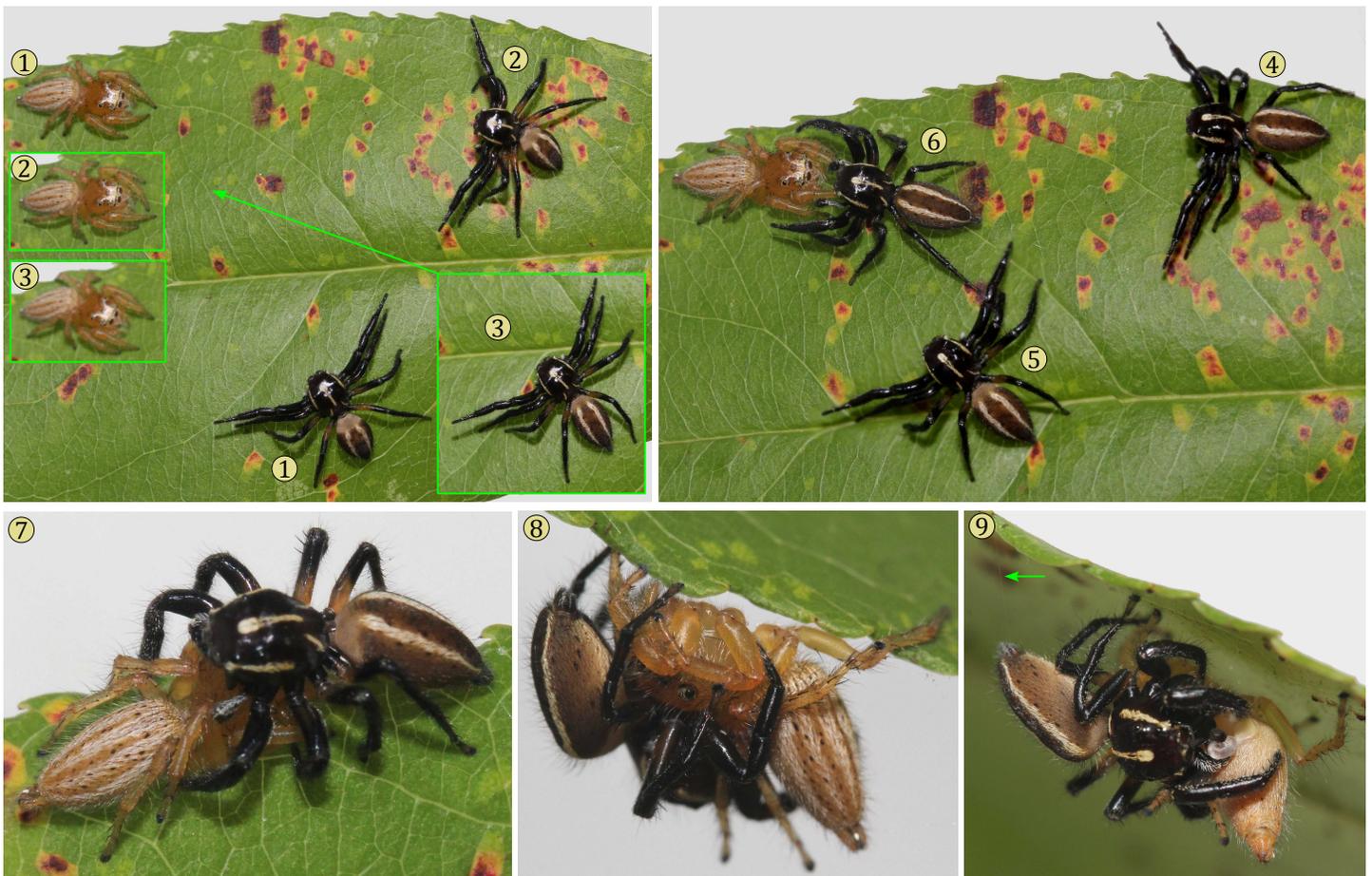


Figure 19. Courtship and mating sequence (1-9) of *C. puerperus*. 1-3, This montage shows how the male initially moved from side to side in front of the female, which turned slightly to follow his movements. 4-6, At the end of the male's zig-zag approach, the female stopped turning and the male advanced to touch her with legs I (6). 7, Male mounting the female, and guiding her with the touch of a leg I to rotate her opisthosoma. 8-9, Two views of the mating pair as they moved to the underside of the leaf. In (9), the male was partly supported by its dragline (arrow).

As shown in Figures 20 and 21, a male *Colonus* would usually mate on one side, then on the other.



Figure 20. Courtship and mating sequence (1-8) of *C. puerperus*. 1-2, Display and approach. 3-4, Mounting and initiation of right-side (both male and female) mating. 5, Right-side mating. 6, Changing sides. 7-8, Two views of left side mating. After mating, the pair separated, and the female would not accept any more suitors.



Figure 21. Left-side (1), followed by right-side (2) mating by a *C. puerperus* pair. In (1) this male secured its hold on the female with its foot pads.

I have observed several instances where a male *C. puerperus* would approach and grapple with a female that was not passive (Figure 22).



Figure 22. Sequence of images (1-4) showing a grappling *C. puerperus* pair. When this happened, the male would approach with pedipalps held to the sides, almost as if engaging in a contest with another male. This male would be in a very vulnerable position (3-4) should the female attack, but I have seen females almost pushed over on their back by grappling males that push forward with their chelicerae, and none of these females attacked the males.

Studies of salticid courtship (see references in Richman 1981; Elias et al. 2012) usually involve the placement of males and females in an arena, most often on a flat horizontal surface. As shown here (Figures 23, 24), male *C. puerperus* would also recognize, display to, and successfully mate with, females approached from other directions.



Figure 23. Male *Colonus puerperus* displaying to a female that it has found on the far side of a stem.

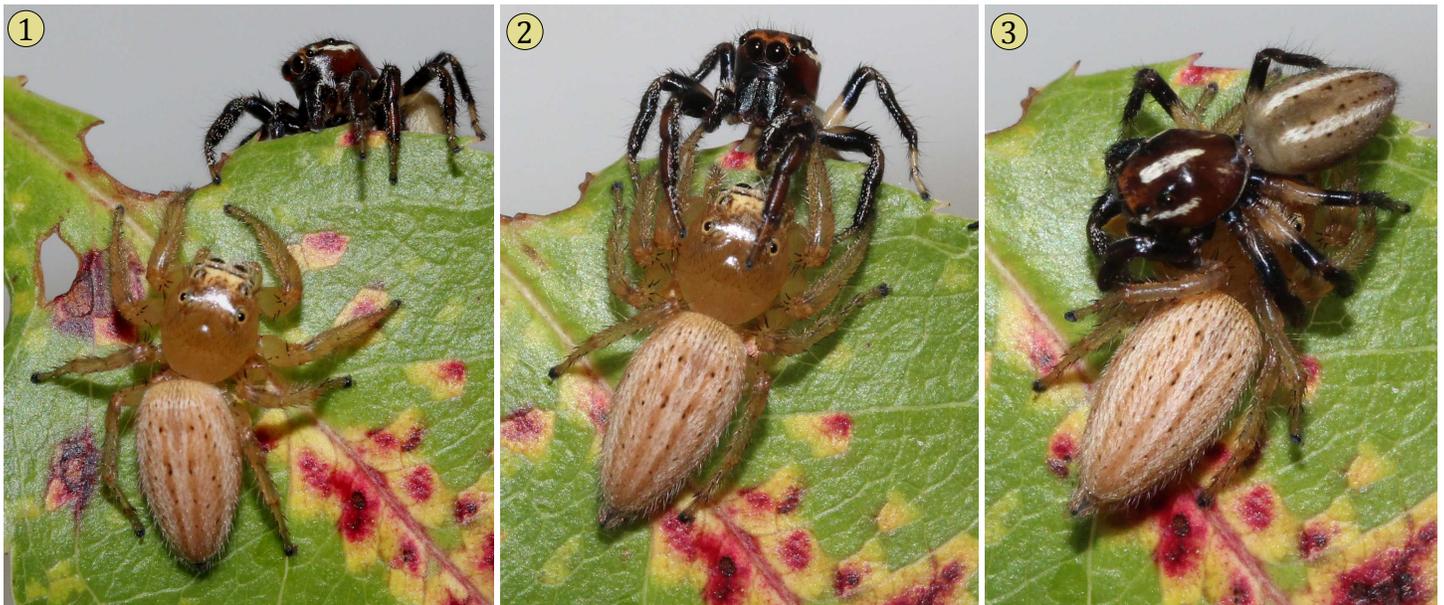


Figure 24. Sequence of images (1-3) showing a male *C. puerperus* locate (1), mount (2), and then successfully mate (3) with a virgin female that was walking on the upper surface of a leaf. In this case, there was no formal display by the male with legs I.

The courtship display of a male *C. sylvanus* is very similar to that of *C. puerperus* (Figure 25). In one example shown here (Figure 26), the male sighted and successfully grappled with a female in a few seconds, with almost no visual display during the approach.



Figure 25. Courtship displays by two different (1-2, 3-4) male *Colonus sylvanus* facing a sighted female in the distance. The extended legs I of a male *C. sylvanus* are relatively long, longer than its body length.



Figure 26. Sequence of images (1-9) showing direct approach by a male *Colonus sylvanus*, with successful mating. 1-4, Approach and mounting. 5-6, Two views of right-side mating. 7, Changing sides. 8-9, Two views of left-side mating.

As noted for *C. puerperus*, *C. sylvanus* males would make a zig-zag approach to a female on a flat surface, and might also grapple with a reluctant or active female (Figure 27). To observe the mating of *Colonus*, I reared immature females caught in the field, thus ensuring that they were virgin. I have never observed mating by either species more than once, and mated females often actively stalked males (particularly smaller males) in both species. Females reared in the laboratory after a single mating successfully reared multiple broods.

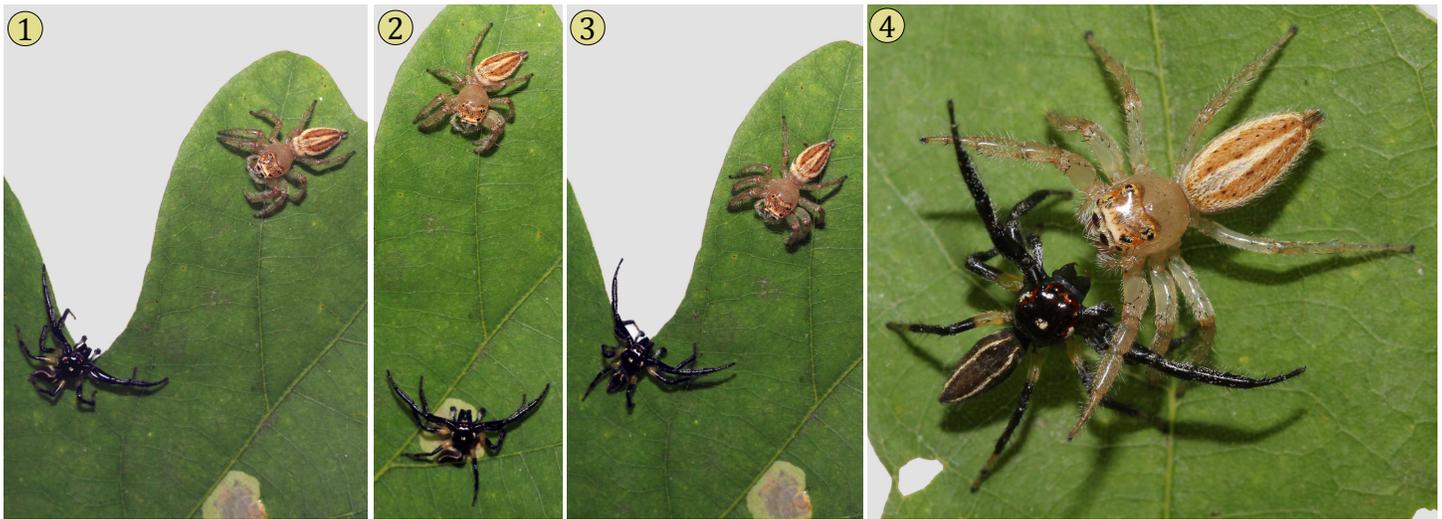


Figure 27. Sequence of images (1-4) showing zig-zag approach to a female by a male *Colonus sylvanus*, resulting in grappling but not successful mating. This female had mated previously.

Brood sacs

I have not found *Colonus* brood sacs in nature, but indoors these appear to be similar to the molting sacs that I have found, bounded by a sheet of silk inside of a rolled leaf, and tightly sealed on all sides. As shown in Figure 28, all of the *C. puerperus* brood sacs were protected with a thick parchment that was initially white, but then became yellowish in color within days of its production. The white brood sacs produced by female *C. sylvanus* were similar in size and structure, but never showed a hint of color.

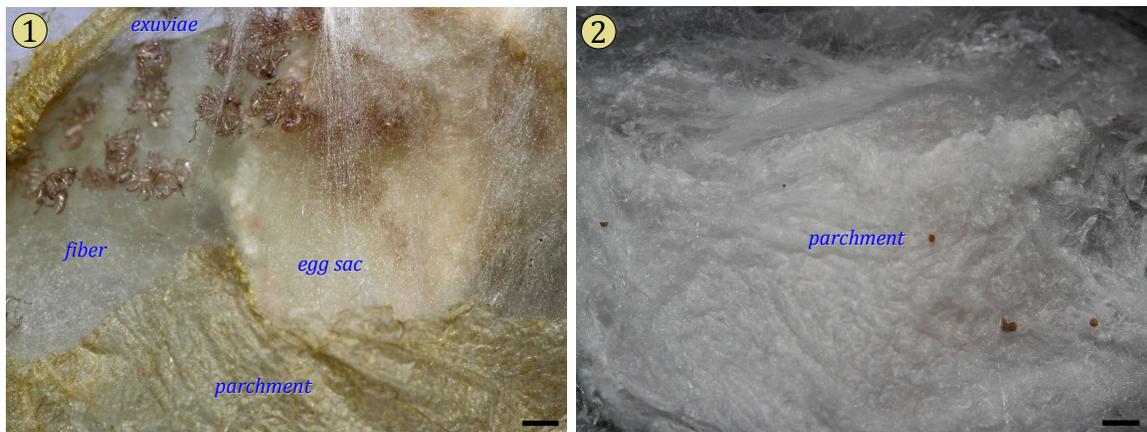


Figure 28. Brood sacs of *Colonus*. **1**, Brood sac of *C. puerperus*, dissected after the young emerged to reveal its inner, fibrous structure, and the thicker silk (egg sac) that was wrapped around the eggs when they were laid. Exuviae I are visible at upper left. Note the thick, yellow parchment layer that tightly sealed this brood sac. **2**, Exterior of brood sac of *C. sylvanus*, showing the thick white parchment layer.

Immatures

Immature *Colonus puerperus* are shown in Figures 29-30. Some of the older spiders shown here were wild-caught, but the younger instars were reared. Most instars of *C. puerperus* and *C. sylvanus* bear a distinctive, large black spot at the center of the ocular quadrangle. Second instars of *C. puerperus* do not. The third instars of *C. puerperus* do have this spot, and are thus much more like the second instars of *C. sylvanus* in appearance. In later instars, *C. sylvanus* get more of the red scales around the eyes that characterize most adults of both sexes, whereas these are not seen in *C. puerperus*. Immature males and females are very similar, and males only assume their dark adult pigmentation *after* their final molt.



Figure 29. Early immature *Colonus puerperus*. **1-5**, Second instars (first emergent stage). The spider in (5) was feeding on a captured nematoceran. **6-10**, Third instars. Apart from their distinctive yellowish coloration, these were almost identical in coloration to second instar *C. sylvanus*, even down to the details of the fine dark marks on the opisthosoma. The spider in (8-9) was feeding on a microlepidopteran. The spider in (10) directly attacked this young thomisid spider with a bite to the rear of the carapace, much as adults attack larger spiders.



Figure 30. Later immature *Colonus puerperus*. **1-2**, The greenish coloration of this fourth instar was related to something that it had eaten earlier. In (2) it had just captured a small spider with a bite to the rear of the carapace. **3**, Fourth or fifth instar feeding on a captured brachyceran fly. **4-5**, Fifth instars (penultimate males) feeding on a brachyceran fly (4) and a thomisid spider (5). *Colonus* commonly use the leg of a spider as a 'straw' through which digestive fluid can be alternately egested and ingested. The spider in (4) had already lost the black (juvenile) spot of the ocular quadrangle, still seen in (5). Apart from their clavate pedipalps, immature males look just like females. These can be distinguished from immature *C. sylvanus* by the lack of red scales around their eyes, but the pattern of their dorsal opisthosoma is very similar.

Second instar *Colonus sylvanus* (Figure 31) are relatively colorless when they emerge from the brood sac, and about 2.0 mm in length, slightly less than the 2.5 mm third instars of *C. puerperus* that they closely resemble. I released a group of these into the woodland understory of our garden, where they naturally occur, and followed them around with my camera for some time. As one climbed up a stem leading to a leaf, an adult female *Lyssomanes viridis* (Walckenaer 1837) rapidly ran across the underside of that leaf and jumped upon the small *T. sylvana*, seizing it in its chelicerae (Figure 31:8). I had not seen this *Lyssomanes* prior to the attack, and *L. viridis*, a common woodland spider in the southeastern United States, is not generally thought to feed on spiders. My own observations suggest, however, that small spiders of all kinds are preyed on by a wide variety of salticids, including the small *Zygoballus* species (*Z. sexpunctatus*; see Hill 2010a). In considering the impact of other spiders on salticid populations, we must remember that most of the success of these animals is based on their ability to survive through a series of immature stages when they are most vulnerable.



Figure 31. Second instar *Colonus sylvanus*. **1-5**, These small (~2.0 mm), transparent juveniles already had the large black ocular spot (juvenile spot) that does not appear until the third instar of *C. puerperus*. **6**, As juveniles wandered on one of our local *Prunus* species, they readily fed (as do many insect and spider species) from its nectaries as shown here. **7**, Second instar with its mother. This picture is included only to show relative size, not maternal care! **8**, Photo of an adult female *Lyssomanes viridis* feeding on a second instar *C. sylvanus* on the underside of a leaf in my South Carolina garden. The woodland habitat and timing of emergence of *T. sylvana* in the spring make them vulnerable to these lurking predators.

As shown in Figure 32, by the fourth instar *C. sylvanus* had those distinctive red-orange to red scales around the eyes. Curiously, just as the detailed pattern of the dorsal opisthosoma of third instar *C. puerperus* was the same as that of second instar *C. sylvanus*, the appearance of the dorsal opisthosoma of later instars of both species was virtually identical, with the distinctive banding of the female *C. sylvanus* opisthosoma only appearing in the adult.



Figure 32. Older juvenile *Colonus sylvanus*. **1-4**, Third instars had white but not red scales around their eyes, and would be difficult to separate from *C. puerperus* at this age by their appearance. However, these were ~4.0 mm in length, compared to the ~2.5 mm length of third instar *C. puerperus* (Figure 28:6-10). **5-7**, Fourth instars had red scales around the eyes, much like adults, but still had the dark juvenile spot of the ocular triangle. **8-10**, Three views of a penultimate male. It is only *after* the final molt that the dark pigmentation of a male *Colonus* appears. Late instars still had a hint of the juvenile spot (as did some adult females), and a pattern on the dorsal opisthosoma that was almost identical to that of *C. puerperus*. The red-orange to red scales around the eyes, and the dark flecks of the posterior and lateral carapace, were only found in *C. sylvanus* juveniles.

The different appearance of the second instar *C. puerperus* came as a surprise. It appeared as if this species has actually added a smaller instar, perhaps to facilitate dispersal (or *r-selection*) in its less permanent environment. However, I did not notice a significant difference in the number of instars of reared spiders (6 or 7 in both species). At the time that I was rearing these spiders, I noticed that *C. puerperus* had larger broods than did *C. sylvanus*, but this result is also dependent on the relative size and feeding condition of the females, and controlled studies will be required to determine if this is really the case.

Predatory behavior

The relatively slow movements of stalking *Colonus* make these spiders good subjects for the study of predatory tactics. In the field, I have observed *Colonus* stalking and/or feeding almost exclusively on other spiders (Figure 33), but when presented with relatively sedentary insect prey in a naturalistic laboratory setting, they have proven to be quite capable of capturing and feeding on these as well. Here I will highlight some of the characteristics of this predatory behavior observed when *Colonus* were placed in the vicinity of prey under artificial lighting in the laboratory.

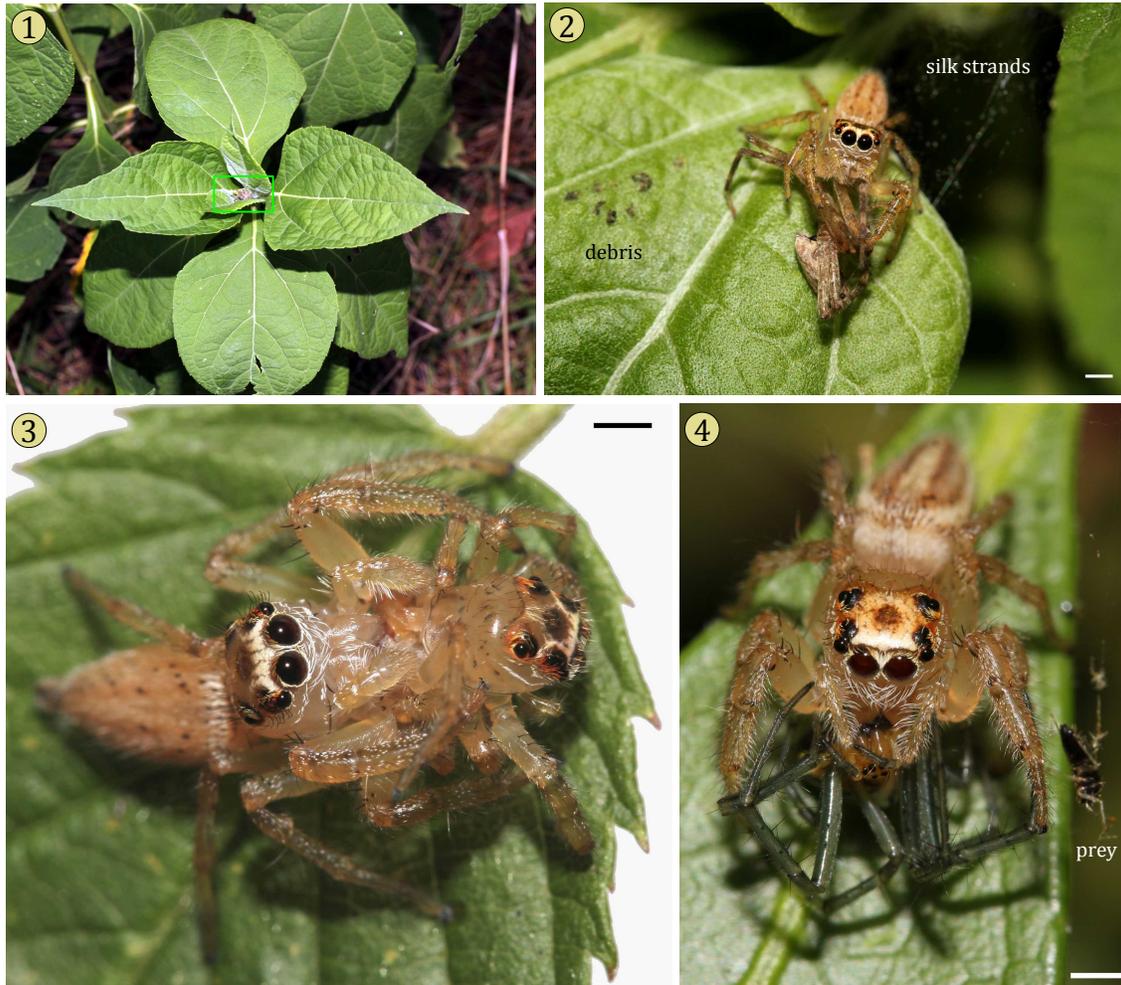


Figure 33. Field records of *Colonus sylvanus* feeding on captured spiders (Greenville County, South Carolina). **1**, Immature (center, inset rectangle) feeding on a captured hunting spider on an herbaceous plant growing at a wooded margin in Greenville County, South Carolina. **2**, Detail of inset in (1). This prey spider was most likely a young *Pisaurina mira*, a species that was often found on the upper surfaces of leaves in this area. The silk strands at the base of this leaf, and the prey debris at left, were similar to those seen at other *Pisaurina* sites. I have also seen an immature *C. sylvanus* of this size jump an adult *P. mira*, but in this case the intended prey reacted quickly and immediately captured and fed on its much smaller attacker. **3**, Penultimate male *C. sylvanus* feeding on a captured conspecific of the same size. This pair was found on an herbaceous plant near a woodland creek, and was brought indoors for this photograph. **4**, Adult female feeding on a captured female *Leucauge venusta* in our wooded garden. In this case I watched the *C. sylvanus* slowly stalk and jump the *Leucauge*, which was hanging upside-down near the edge of a larger web also occupied by a male of the same species. An insect (prey, at right) had been previously trapped in this web, and its struggles may have brought the female *Leucauge* to a position where it was vulnerable to attack by the *Colonus*. I have also seen an immature *C. puerperus* feeding on an immature *Phidippus clarus* in an old-field habitat where *P. clarus* were very common.

Targeted jumps. Many descriptions of salticid attack behavior are based on the short jumps of these animals on flat, horizontal surfaces (Figure 34). Where a direct approach is not possible, however, a longer jump may be in order (Figure 35). *Colonus* can accurately hit prey with very fast upside-down jumps *almost directly toward* the prey position (Figures 36-37). In addition, a *Colonus* that is concealed on the top of a leaf can execute a very rapid jump to capture prey on the underside of that leaf (Figure 38), a remarkably complicated maneuver.



Figure 34. Adult male *Colonus sylvanus* before (1) and after (2) a short jump to capture a moving hemipteran. This *Colonus* rubbed this prey against the leaf surface to remove its defensive spicules before macerating it.

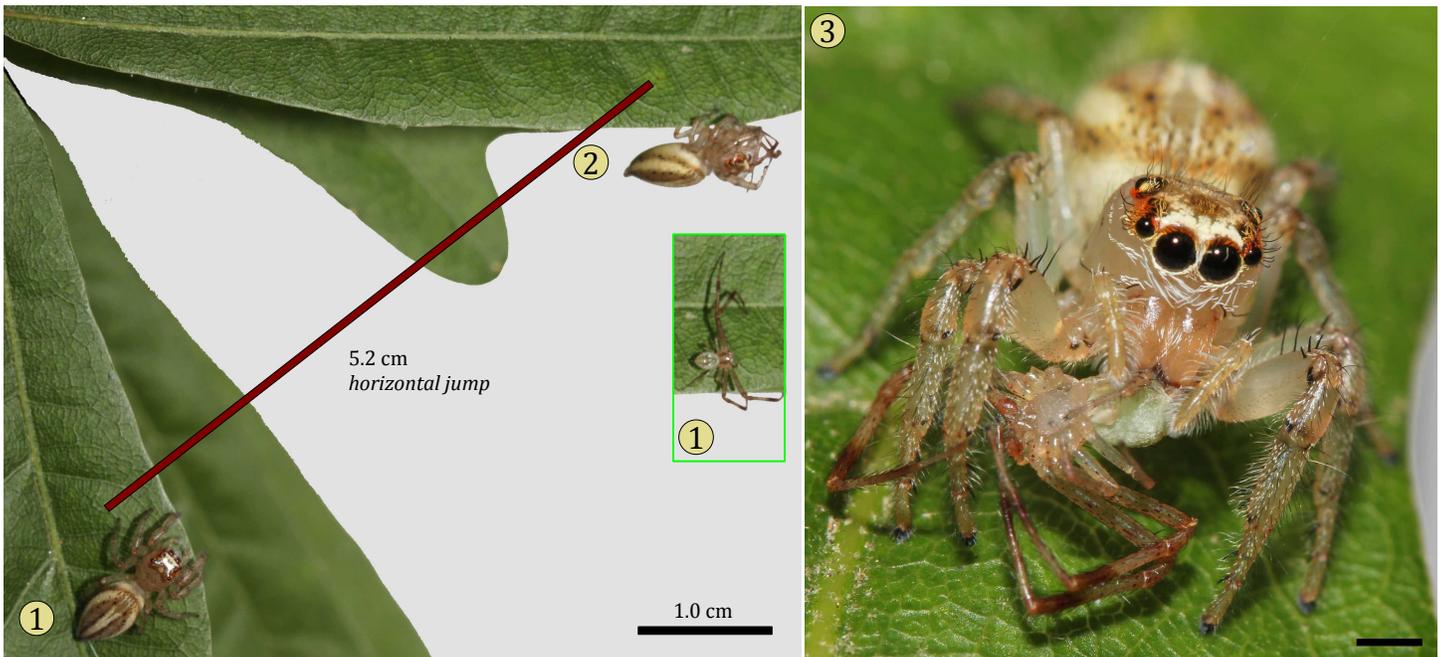


Figure 35. Horizontal jump by an adult female *C. sylvanus* to capture a small spider. The montage at left shows two sequential positions of the spider and its prey, before (1) and after (2) the jump, as viewed from above. **3**, Later view of this spider macerating the opisthosoma of this prey.



Figure 36. Upside-down jump by an adult female *C. sylvanus* to capture an immature *Leucauge venusta* resting beneath a leaf. **1**, Stopping to watch the prey during a slow approach. **2**, Ready for the jump. **3**, Holding the *Leucauge* by its carapace immediately after this jump. **4**, Later view of this spider feeding through one leg. To hit this target at a distance of about 3 cm, this *Colonus* had to make a very fast, almost direct jump close to the underside of the leaf.

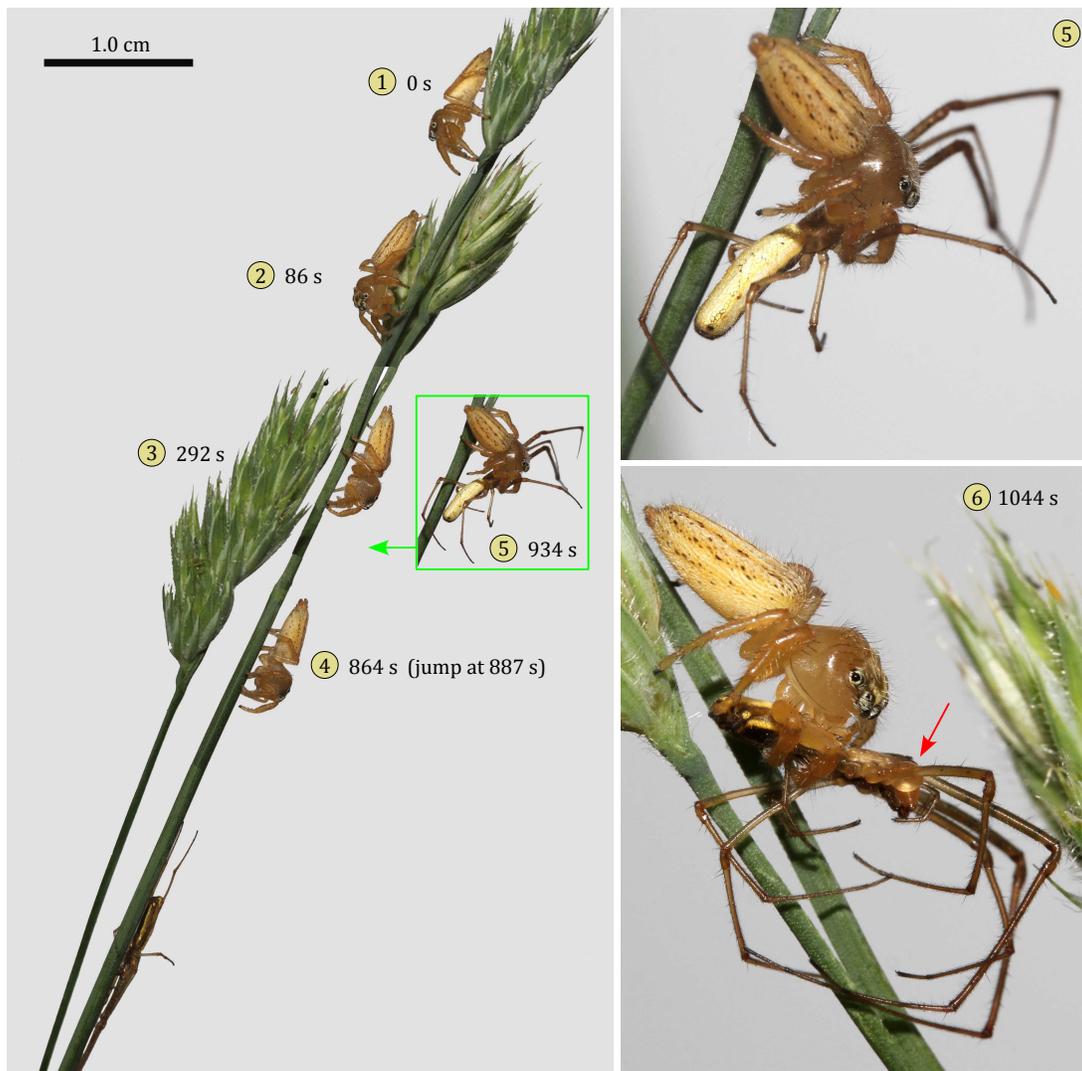


Figure 37. Photomontage of sequence (1-6) depicting pursuit and capture of a resting *Tetragnatha* by a female *Colonus puerperus*. **1**, Beginning of pursuit. **1-4**, Slow pursuit of more than 12 minutes duration. **4**, Position from which the *Colonus* jumped. **5**, Position after capturing the prey and climbing up the dragline. **6**, Later view of *Colonus* feeding on this prey, showing the site of injury to the carapace of the *Tetragnatha* from the jumping attack (arrow).



Figure 38. Jump to the underside of a leaf by an adult female *C. sylvanus* to capture a resting *Leucauge venusta*. **1**, looking at the prey before jumping. **2**, Holding the prey immediately after jumping around the leaf edge. **3**, Holding the prey after returning to the top of the leaf. **4**, Later view of this spider feeding. Before moving onto this leaf, the *Colonus* had seen this *Leucauge* at a distance. Before jumping (1) very little of the prey animal was directly visible. The jump itself was a 'flip' around the edge of the leaf with legs RIII and RIV holding the edge of that leaf after the jump (2).

As shown in the time sequence for the images in Figure 37, the pursuits of a *Colonus* can be very time-consuming. Slow and often imperceptible movement can require much patience on the part of the observer, but the slow pace at which events present themselves also allows one to see many details. It is fair to say that these spiders are, in general, not *fast chasers of moving prey*, but rather *very slow stalkers of immobile prey*. Their jumps are generally very accurate, usually hitting a target spider with chelicerae affixed to the carapace in a manner that does not allow that spider to retaliate with its own chelicerae.

Use of the dragline as a bungee cord. I have previously (Hill 2010b) described braking on the dragline during the predatory jumps of *Phidippus*. In many of the jumps of *Colonus*, elastic recoil on the braked dragline (*bungee effect*) appeared to help the predator pull its prey off of a surface (Figures 39-41).

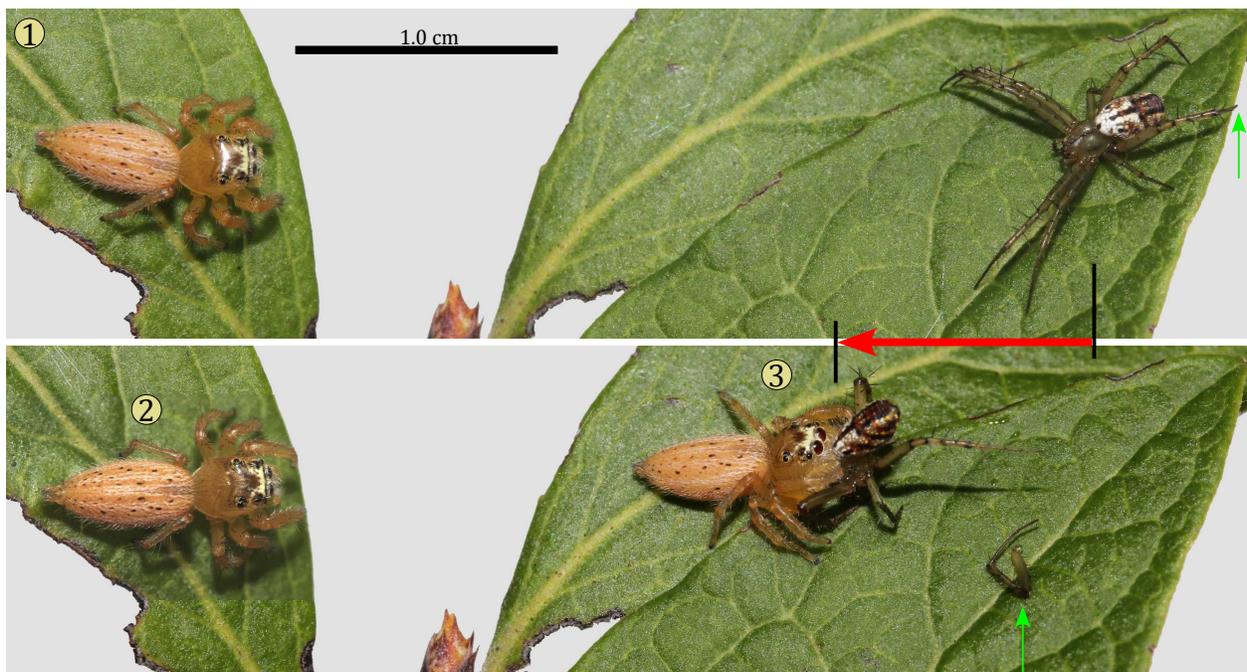


Figure 39. Sequence (1-3) showing the attack of a female *C. puerperus* on a resting spider. Note the hold on the leaf edge by the prey (green arrow, top right) prior to the attack. **2**, Position of *Colonus* when it jumped. **3**, Position immediately after jump, with taut dragline (not shown). Note the autonomized limb of the prey spider after this attack (green arrow, lower right). The bold red arrow shows the ~1 cm of recoil after this prey was secured by the attacking *Colonus*. This recoil may have helped to dislodge the prey from its hold on the leaf edge.



Figure 40. Another sequence (1-2) showing the attack of a female *C. puerperus* on a resting spider. The bold red arrow shows the recoil that reversed the momentum of this jumping *Colonus* during its attack, effectively pulling the prey away from its hold on the leaf edge. The jumping position (1) has been added to the lower image to show its relationship to the post-jump position (2).



Figure 41. Sequence showing the attack of an immature female *Colonus puerperus* on a penultimate male *Oxyopes salticus*. 1-2, slow stalk to arrive at the jumping position (2), covering about 1 cm in 3 minutes. 3, Position immediately after the jump. 4, Later view, showing the hold of this *Colonus* on the rear carapace of the *Oxyopes*. Prior to this attack, the *Oxyopes* held one of its legs in an erect position, typical for this spider. *Oxyopes* often reacted quickly to the attack of a *Colonus* and escape with their own spring-like jump. In this case, the position after the attack (3) appeared to combine the recoil (*bungee force*) of the *Colonus* on its dragline with the forward momentum of the springing *Oxyopes* (up and to the left in this view). Note the widely extended legs of the captured spider (3).

When I was recording videos of the behavior of *Colonus sylvanus* several years ago, I noticed that some spiders would produce a chain of 'connected silk balls' with their dragline when resting in place (Figure 42). I have observed little of this behavior since, and it is possible that only some *Colonus* individuals do this. This behavior could relate to the effectiveness of the *bungee effect* in these spiders, and it is something to look for in future studies.



Figure 42. Frame from video showing (arrow) small silk balls spun on the dragline of an adult female *Colonus sylvanus*. Some individuals will produce a long chain including many of these balls, but their function is not known.

Use of detours during the pursuit of prey. The use of indirect routes, or detours, has been reported for many salticids, including *Colonus* (Hill 2010a). The general features of this behavior include visual determination of available access routes and movement toward those access routes, interrupted by turns (*reorientation turns*) to face the expected position of the prey. In *Colonus*, all of these behaviors can be observed, in slow motion (Figures 43-44).

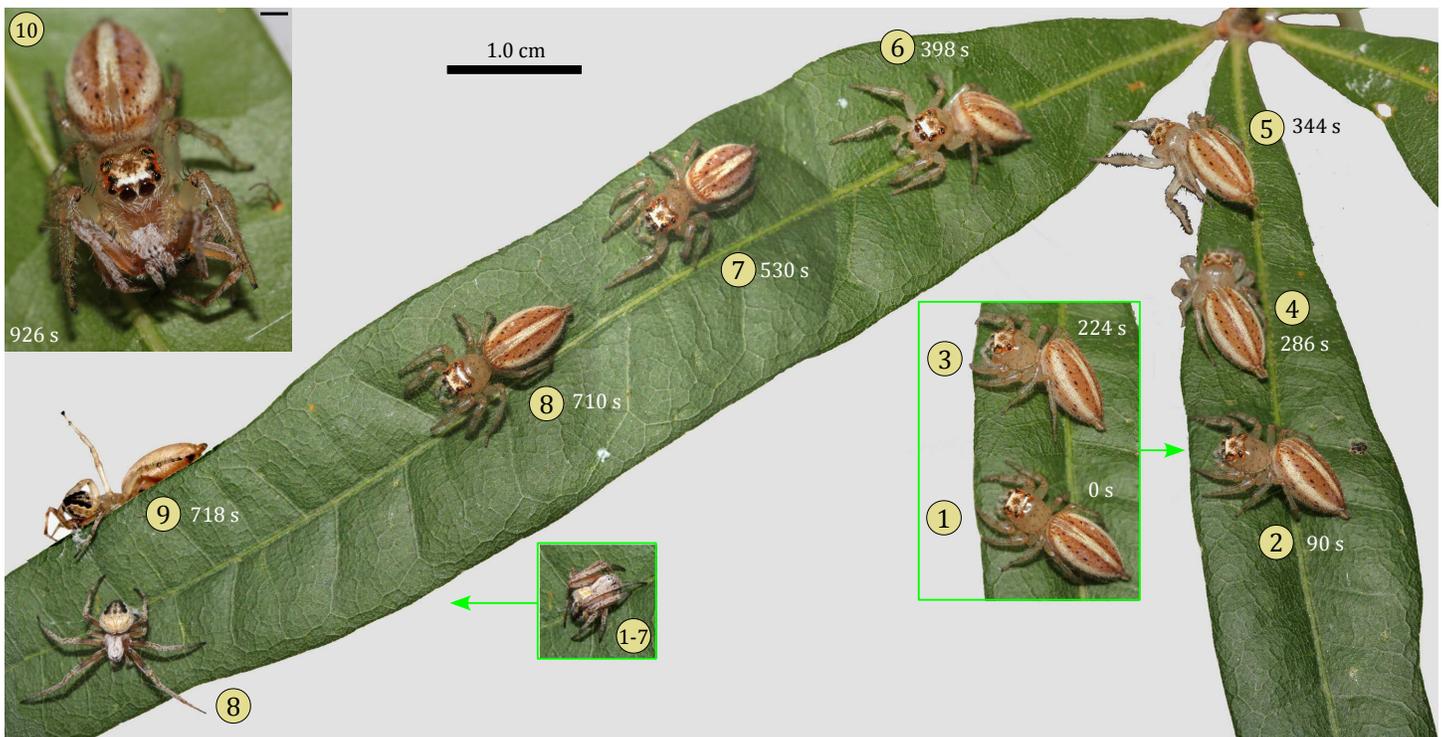


Figure 43. Photomontage (sequence 1-10, viewed from above) showing some positions associated with the slow, detoured pursuit of an araneid spider by an adult female *Colonus sylvanus*. When first sighted by this *Colonus*, the araneid was crouched and immobile, facing toward the stem of this plant. When it began to move (8), the *Colonus* attacked and captured it. 1-4, Turns to face the access route alternated with turns to face the prey, and forward movement.

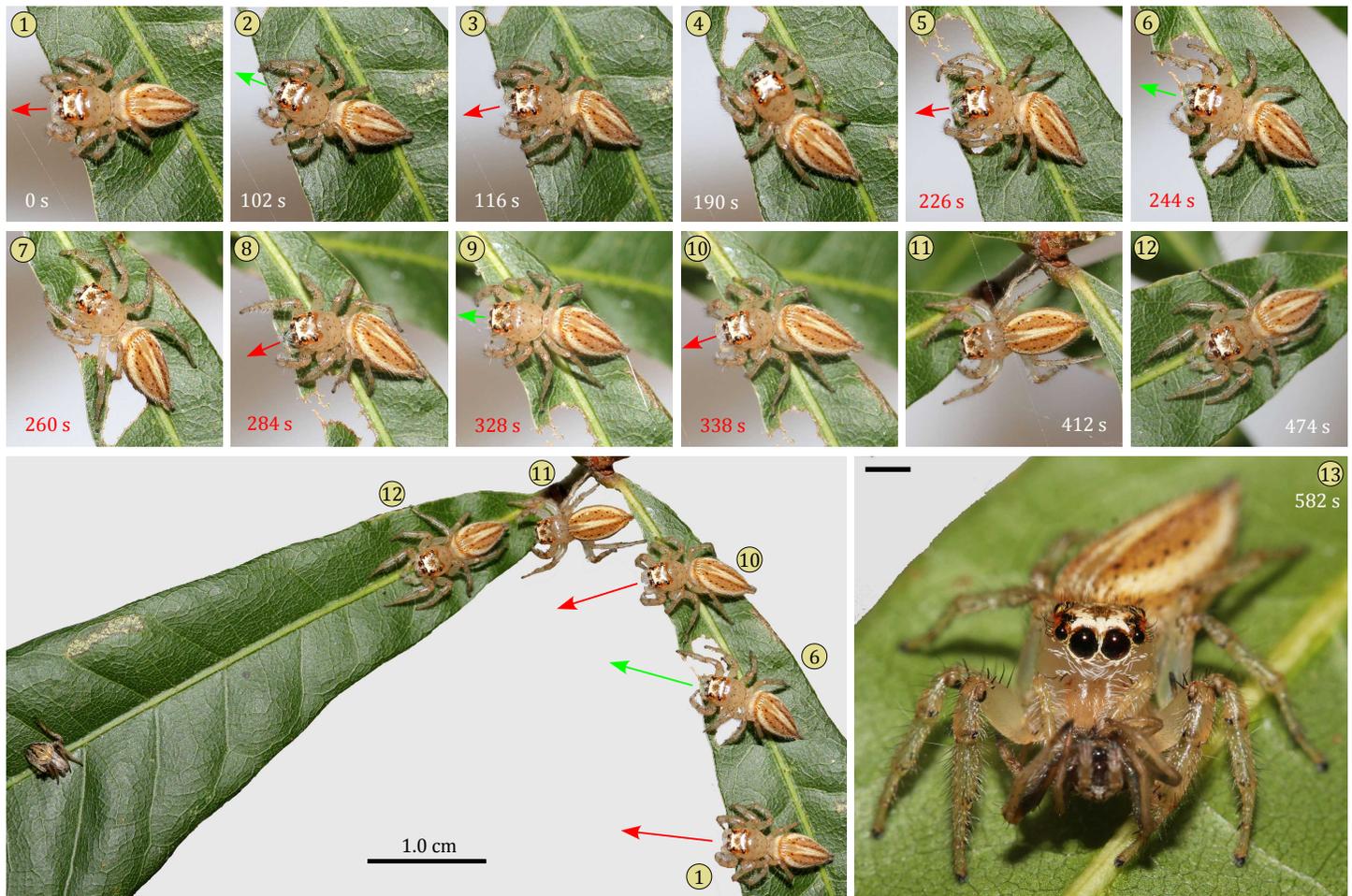


Figure 44. Some of the positions (sequence 1-13, viewed from above) associated with the slow, detoured pursuit of an araneid spider by an adult female *Colonus sylvanus*. Turns to face the prey are marked with red arrows, and turns to face the access route are marked with green arrows.

In some cases, a jump may be used by a *Colonus* (as in *Phidippus*; Hill 2010a) to reach a sighted access route (Figures 45-46). The ability of these spiders to determine the relative prey position after a long access jump (Figure 46) requires them to integrate information related to the distance and direction of an access jump with the original distance and direction of the prey, to determine the location of the prey after the jump is completed. I actually think that this ability is more sophisticated than this, and, at the risk of appearing to apply an anthropocentric bias to this subject, I would propose that the analysis of this behavior can be advanced if we hypothesize the use of discrete *operating concepts* (or just *concepts*) by the hunting salticid. Just as we employ concepts in our own reasoning, we can define an operating concept as follows: An *operating concept* represents a *fact* about the situation of a spider that has a specific impact on its behavior, and the use of this fact is *implicit* in the behavior of the spider. In future research, we can design experiments to test the validity of each hypothesized operating concept. Some relevant examples are shown in Table 1.

Table 1. Some hypothetical operating concepts relevant to salticid behavior. This is a small selection of the possibilities.

behavior	implicit operating concept
rapid jumping attack to opposite side of leaf	prey is on the opposite side of this leaf
facing up in prey direction after jumping to stem	prey is resting higher up on this stem
facing leaf cluster associated with prey	prey is on that leaf cluster
not jumping at prey 8 cm overhead	prey at this relative height is out of range
jumping directly at prey 8 cm below	prey at this relative height is in range

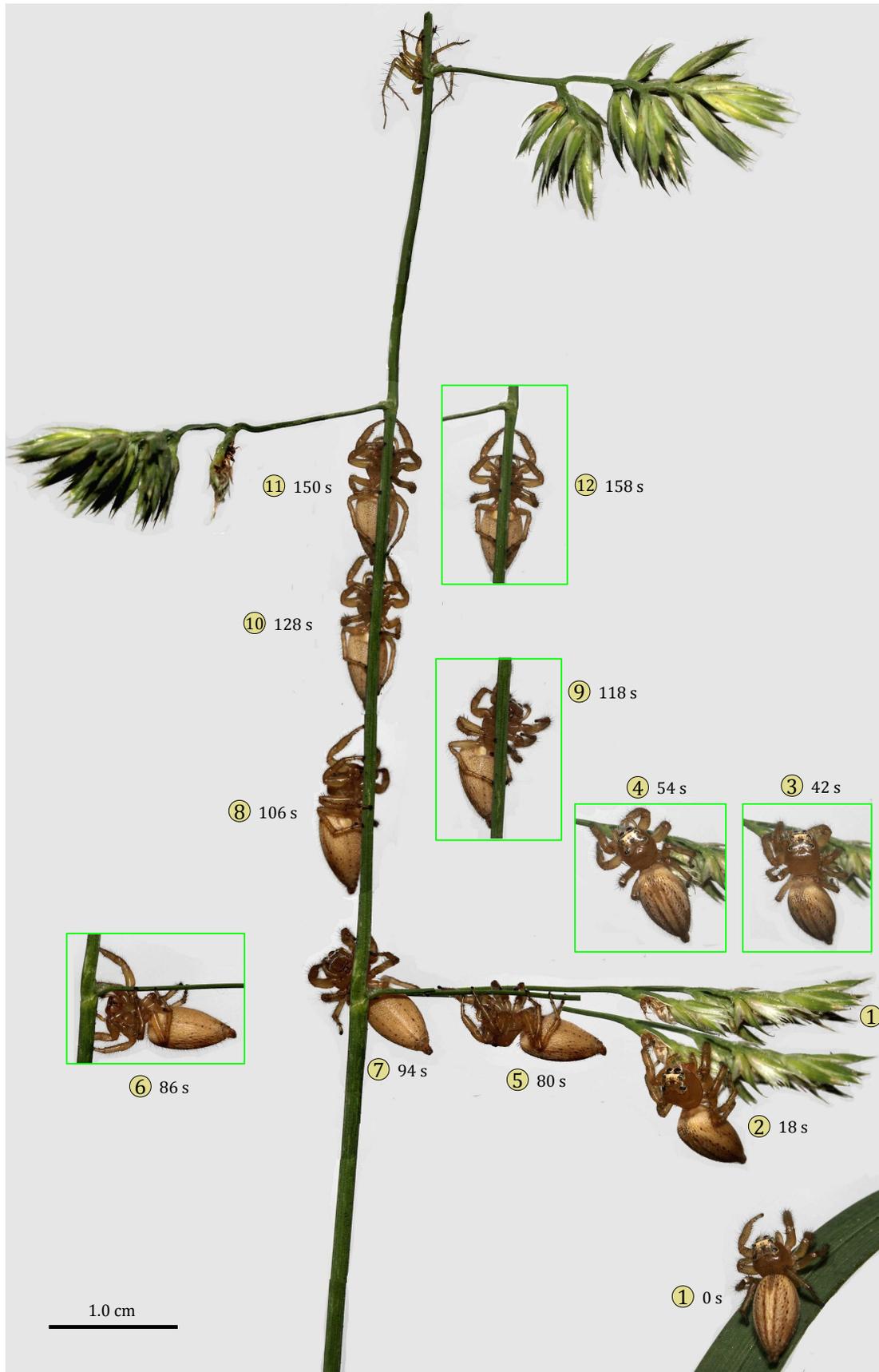


Figure 45. Sequence (1-12) depicting the pursuit of an alert *Oxyopes salticus* at the top of a grass stem by an adult female *Colonus puerperus*. Multiple positions of the branch at lower left are presented to show how this was pulled down when the spider jumped to it (2). **11-12**, Two sequential positions of back and forth rocking movement by the *Colonus* at the start of a very slow advance up the stem.

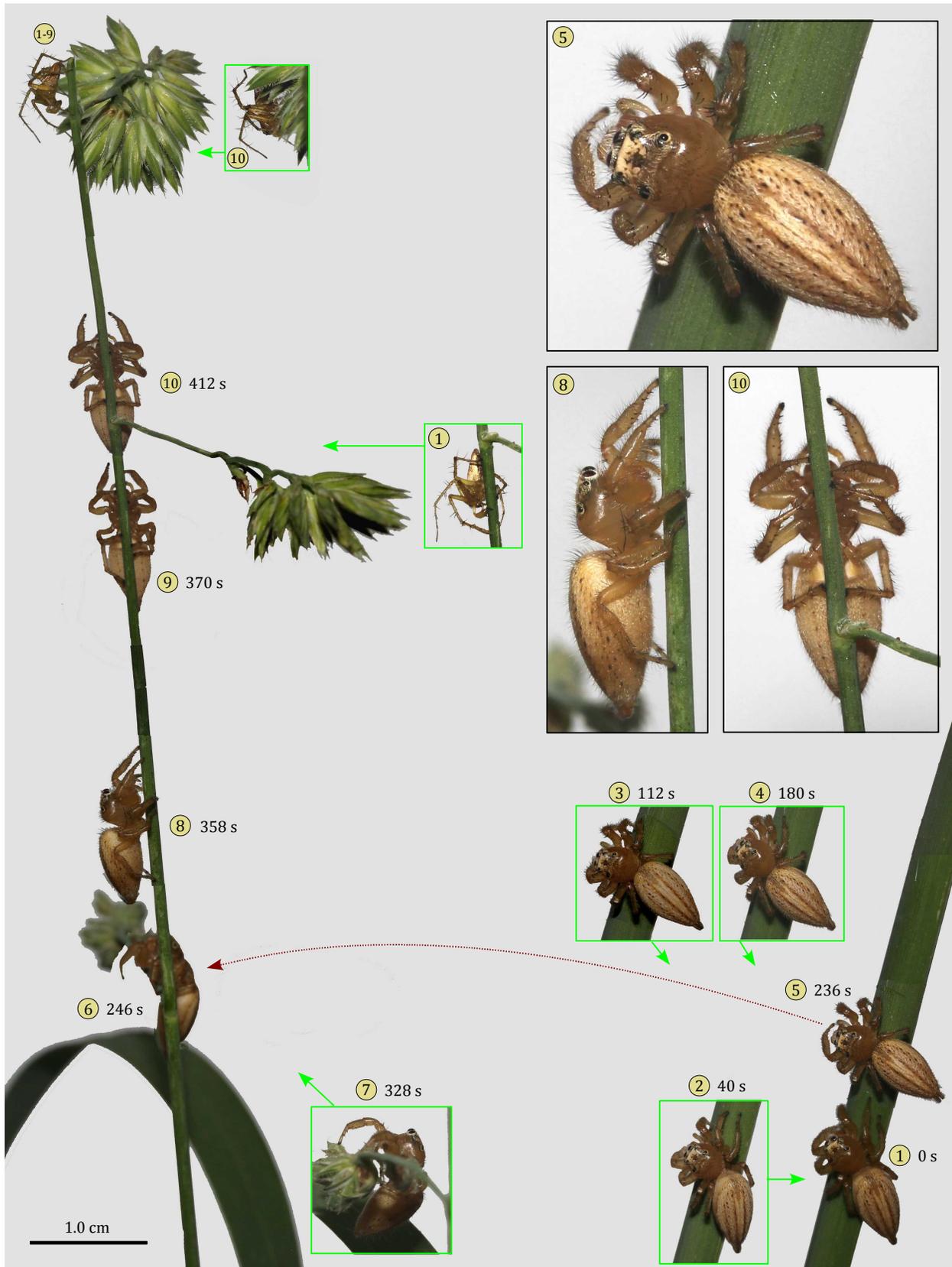


Figure 46. Sequence (1-12) depicting the pursuit of an *Oxyopes salticus* at the top of a grass stem by an adult female *Colonus puerperus*. This *Oxyopes* was in a lower position (1) when sighted by the *Colonus*. **1**, Facing the original prey position. **2**, Turning to face the stem. **3**, Facing the stem from a higher position. **4**, Facing the expected prey position. **5**, Preparing to jump to the stem. **6**, Position after the jump, on a small branch. **7**, Facing the prey position. **8-9**, Advance toward the prey position. **10**, Preparing to jump to the prey. Note the balanced medial placement of legs IV on either side of the stem to power this jump. At this point the *Oxyopes* moved toward the *Colonus* (inset, 10), then quickly jumped away.

In the example shown in Figure 47, a female *C. sylvanus* moved down to a stem, then slowly moved up and around to the opposite side of that stem where the spider that it had sighted was located.

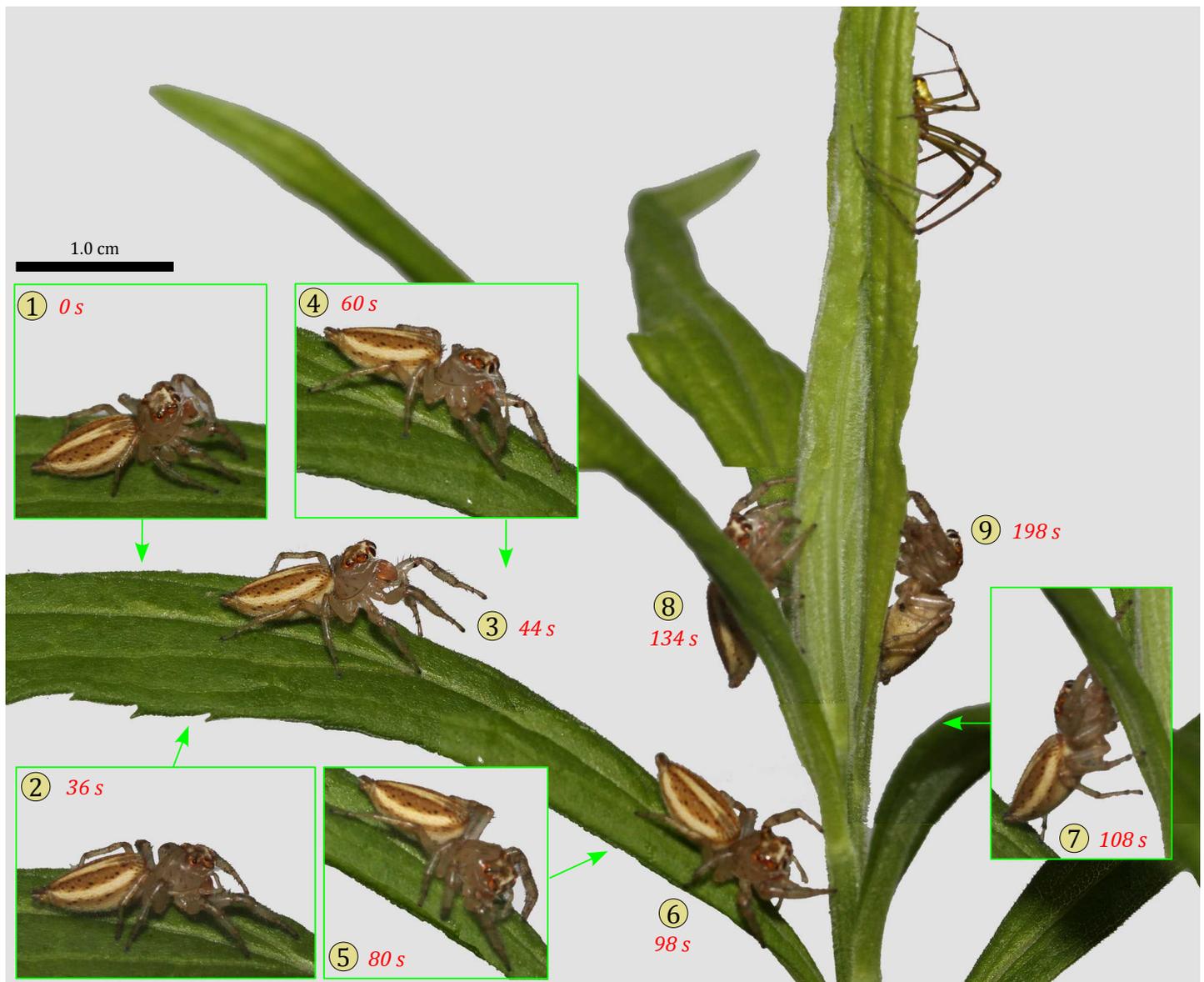


Figure 47. Sequence (1-9) depicting a pursuit by an adult female *Colonus sylvanus*. **1**, Facing the prey. Very little of this immobile prey could be seen from this position, but the spider initiated pursuit. **2**, Movement down toward the stem. **3**, Reorientation to face the prey position. **4-7**, Movement to the stem. **8-9**, Slow movement up and around the stem to face the prey.

Rocking or swaying during the approach to prey. I first observed *rocking* or *swaying* behavior as an adult female *Colonus sylvanus* stalked a *Leucauge venusta* (Hill 2007c). *Colonus* do not vibrate their pedipalps as do many other salticids as they approach prey, but they frequently rock forward and backward (Figures 48-51) as they approach, at a rate of about 0.5-2 cycles/s. I have seen adults and immatures, and both sexes of *C. puerperus* and *C. sylvanus*, engaged in *rocking* and (when side-stepping during an approach) *swaying* from side to side. At the same time, it is not certain what triggers this behavior, which is sometimes, but not always, seen during the approach to either insect or spider prey. I have observed a similar gait in chameleons (*Chameleo jacksoni*) and mantids (*Stagmomantis carolina*). This appears to be cryptic movement, although in mantids swaying may also play a role in distance estimation. A form of *cryptic stalking* has been described for the salticid *Portia fimbriata*, but was observed only during the pursuit of salticid prey. This was described as a *slow and choppy* movement that keeps salticid prey from

recognizing the attacking *Portia* (Jackson & Blest 1982; Harland & Jackson 2000). A slowly stalking *Colonus* will move quickly if one blows on it to emulate a breeze, or otherwise moves or vibrates the plant on which it is walking. Considering the many breezes and microcurrents in a natural environment, predatory pursuit there can be expected to be much faster than that observed in the laboratory, where the air is stationary.

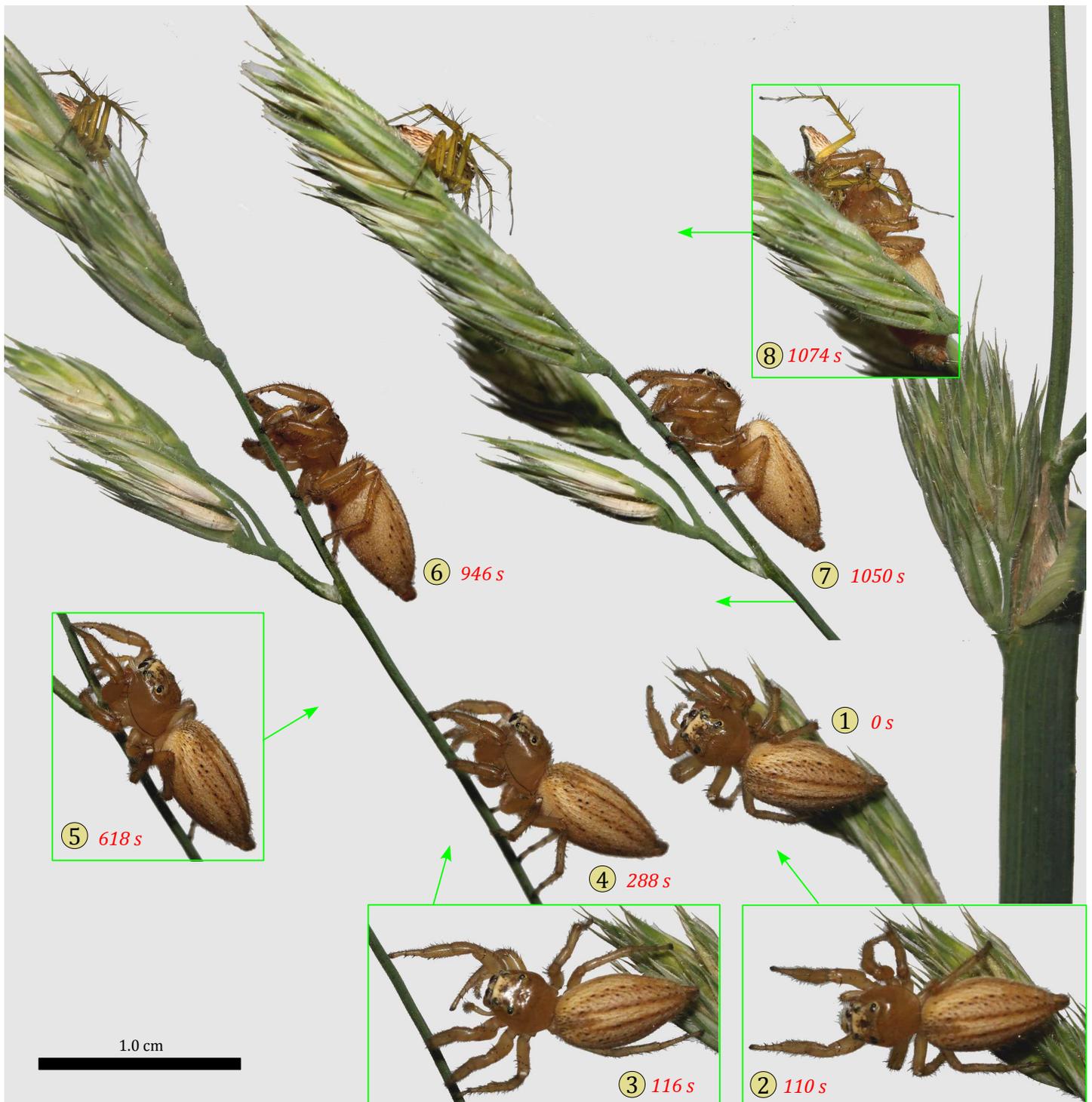


Figure 48. Sequence of images showing pursuit and capture of an *Oxyopes salticus* by an adult female *Colonus puerperus*. The entire sequence took more than 15 minutes to complete. Slow movement between (1) and (4) is depicted in Figure 49, and rocking movement between (5) and (6) is depicted in Figure 50. This spider jumped from position (7) to impale the carapace of the *Oxyopes* with its chelicerae. The ability of *C. puerperus* to power an accurate, balanced, upwards jump with legs IV (7) on a thin stem like this is remarkable.



Figure 49. Sequence (1-6) showing slow movement of a female *C. puerperus*, between positions (1) and (4) in Figure 48. Movement of leg RIV, then RIII, took about 2 minutes to complete.



Figure 50. Sequence (1-8) showing some of the back-and-forth rocking movement of a female *C. puerperus*, between positions (5) and (6) in Figure 48. Each back-and forth cycle took about 0.5-2 s to complete. Note the constant position of leg LIV during this movement.

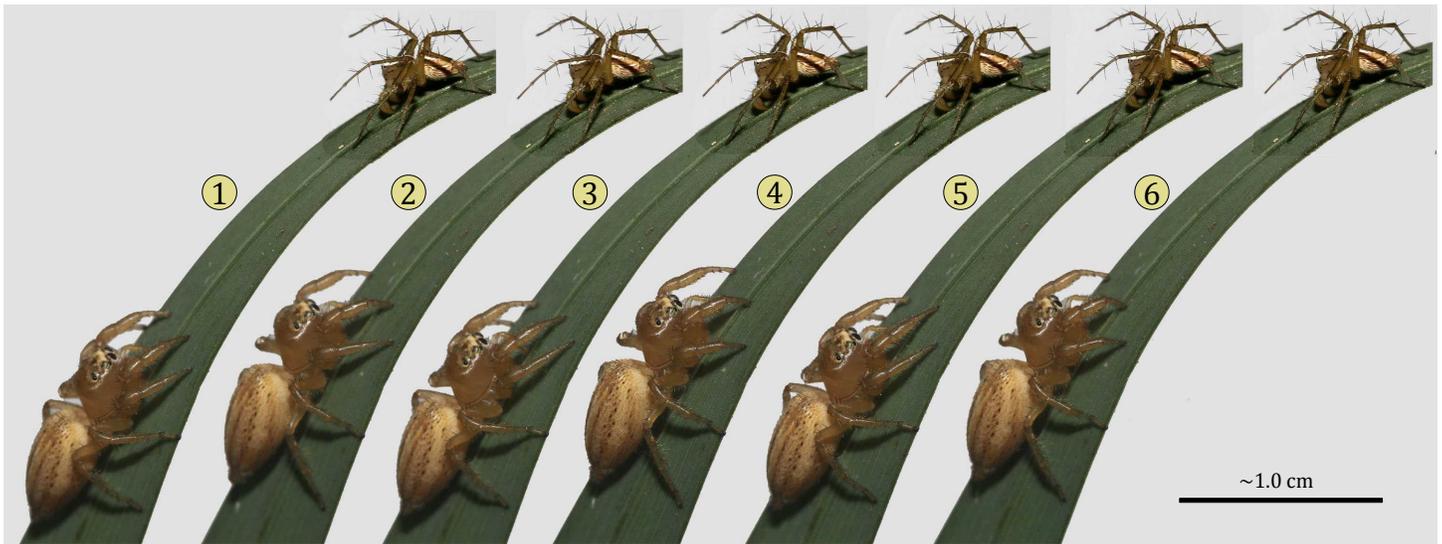


Figure 51. Sequence (1-6) showing some of the back-and-forth rocking positions of an adult female *C. puerperus* stalking an *Oxyopes salticus* on a blade of grass.

Concealed approach to prey. Just as some *Phidippus* will advance toward prey on the opposite side of a branch or stem (Hill 2010a), *Colonus* will often stay out of the view of their prey as they pursue it (Figures 52-54). I have observed this kind of behavior often enough to think that concealed approach, when possible, is a regular feature of the attack program of *Colonus*. This subject is worthy of further study.



Figure 52. Sequence (1-5) showing slow pursuit and capture of a *Leucauge venusta* by an adult male *C. puerperus*. At (1) and (2) this *Colonus* faced its prey for many minutes. 2, Advancing toward the prey in a concealed position on the underside of a leaf. 4, Preparing for a successful upside-down jump. 5, Hanging from the dragline with the captured prey.

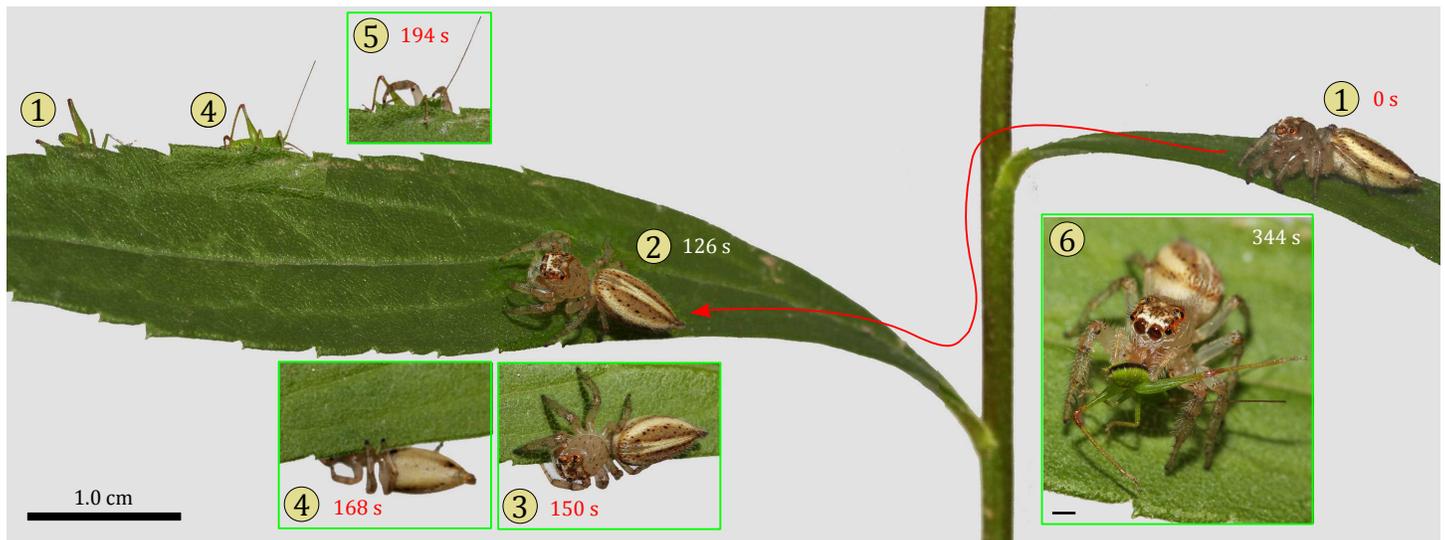


Figure 53. Sequence (1-5) showing pursuit and capture of a field cricket (Tettigonidae) by an adult female *C. sylvanus*. After sighting its prey (1), this *Colonus* advanced along the edge of the leaf opposite to that occupied by the cricket, somewhat out of sight (2), then went under the leaf (3-4) to capture its prey (5) with an upside-down jump.

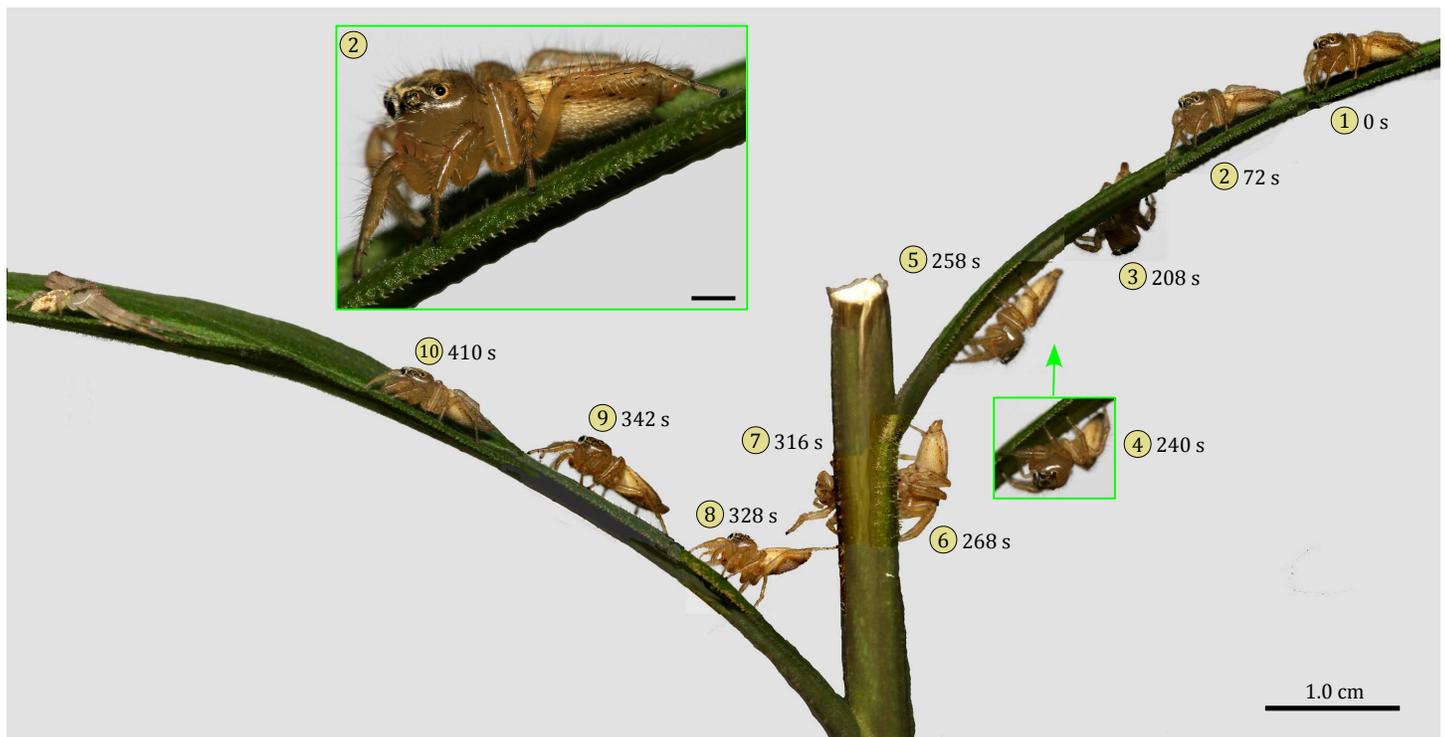


Figure 54. Sequence (1-10) showing pursuit of a thomisid spider by a penultimate female *C. puerperus*. At (3) this *Colonus* moved to the underside of the leaf, then reoriented (7) to the prey position before (8) very slowly stepping onto the leaf occupied by that prey. At (9) the *Colonus* appeared to rear up off of the surface to face its prey, then (10) slowly proceeded toward that prey in a low stance. A low stance like this (10) was commonly observed when a *Colonus* was close to its prey.

Capture of moving prey. Although *Colonus* can actually move as fast as other salticids, I have not seen them aggressively attack moving prey, such as flies, as would a typical *Phidippus*. *Colonus* have a strong ability to recognize stationary prey, and, as noted previously, they approach that prey with great 'stealth', and then jump it quickly and accurately. This is the kind of attack that is suited to the selection of many hunting or web spiders as prey. However, during a slow and methodical approach, the prey may move rapidly toward a *Colonus*, which is quite capable of taking advantage of the situation (Figures 55-56).



Figure 55. Sequence (1-4) showing interaction of a juvenile mantid (*Stagmomantis carolina*) with an adult female *Colonus sylvanus*. **1**, The *Stagmomantis* and *Colonus* sighted each other. **2**, As the *Stagmomantis* rapidly moved toward the *Colonus*, apparently viewed as its prey, the *Colonus* prepared to jump. **3**, After both jumped, the *Colonus* flipped into an upside-down position under its leaf with the *Stagmomantis* in its chelicerae. **4**, Later view, showing the hold of this *Colonus* on her prey. Surprisingly, there was no apparent damage to the *Colonus* from this dangerous encounter, considering the relative strength of the mantid's raptorial appendages.



Figure 56. Sequence (1-4) showing capture of a running *Tibellus oblongus* by a female *Colonus puerperus*. **1**, The *Colonus* had been stalking this *Tibellus* for several minutes. **2**, The *Colonus* continued to advance slowly as the *Tibellus* began to run along the stem. **3**, The *Colonus* then captured the running *Tibellus* with a bite to the carapace, without moving from its position.

Thomisid spiders as prey. Thomisids can be very dangerous to relatively large bees and wasps that approach from the front, but they are very vulnerable to the accurate attack of a *Colonus* that approaches from the rear, where the thomisid has no protection (Figures 57-59).

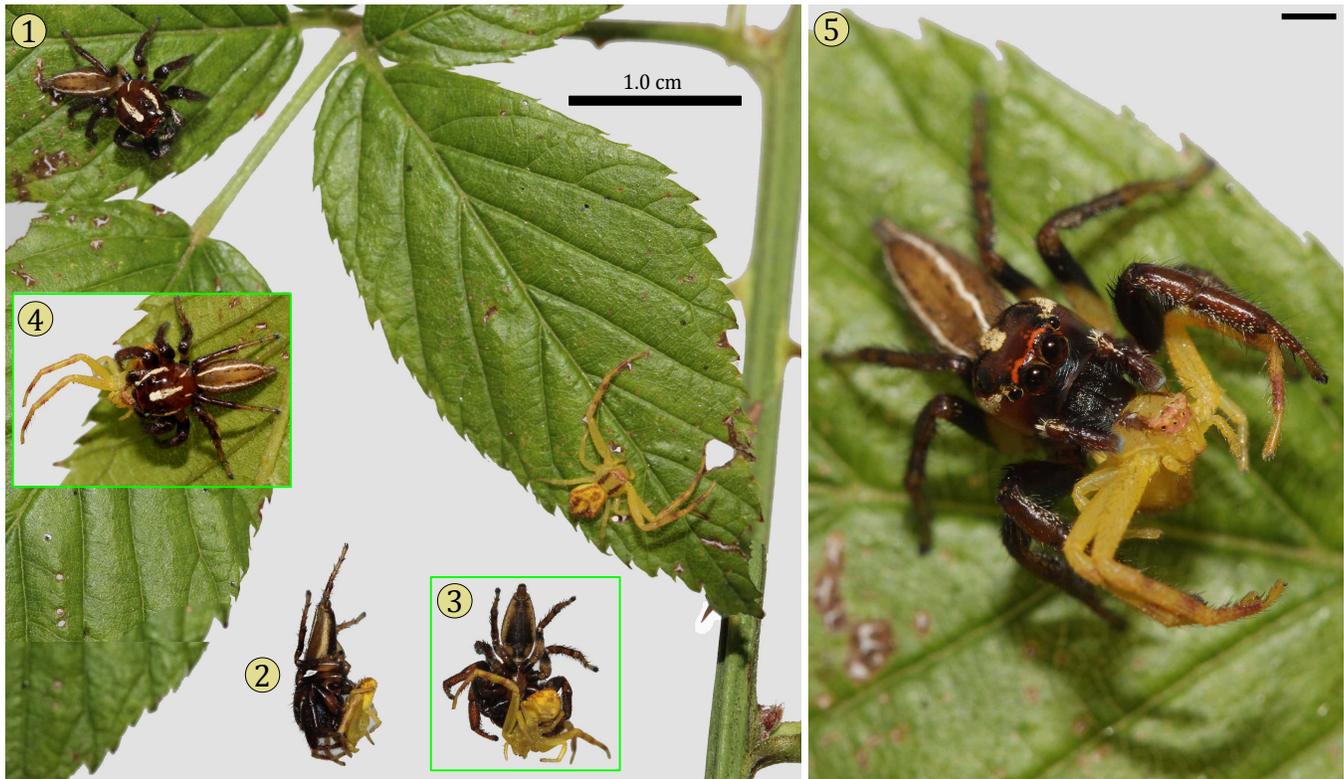


Figure 57. Sequence (1-5, lateral view) showing the capture of a *Mecaphesa* (Thomisidae) by an adult male *Colonus puerperus*. 2-3, Two views of this hanging *Colonus* holding his prey with a bite to the carapace.

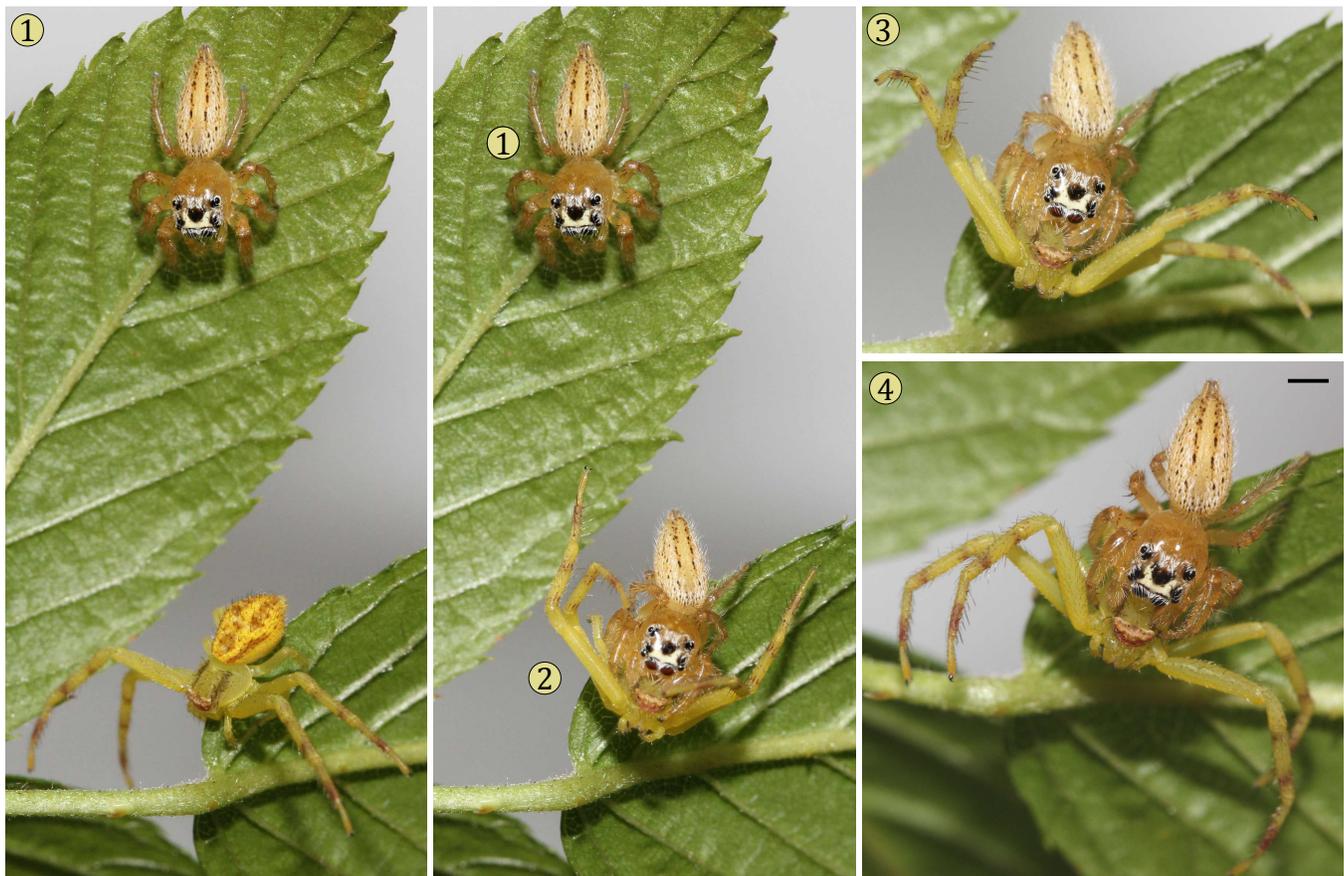


Figure 58. Sequence (1-4, lateral view) showing the capture of a *Mecaphesa* by a penultimate male *Colonus puerperus*, jumping from above to seize the carapace of its prey with its chelicerae. 2-3, Immediately after the attack, the *Mecaphesa* reached for its attacker with its powerful legs I and II, but the attacker was out of its range. 4, Later, legs I and II of this thomisid assumed a relaxed position. Position (1) is repeated in the second frame for reference.



Figure 59. Sequence (1-4) showing the capture of a *Mecaphesa* by an adult female *Colonus puerperus*. Although the prey was not turned away from this *Colonus* at the onset of its jumping attack (1), the attacker was able to use enough pitch in its jump to bite the carapace of the *Mecaphesa* from the rear. Note movement of leg LIV (arrows, 2-3) by the *Colonus* to secure a foothold at the edge of the leaf. Once this *Mecaphesa* relaxed its hold on the leaf with legs III and IV, the *Colonus* flipped it over to macerate the soft opisthosoma (4).

Frontal attacks on thomisids are more dangerous, but the speed of the attacking *Colonus* can prevail if the thomisid is small, or if the thomisid does not assume a defensive posture with legs I and II held *above* the body (Figures 60-62).

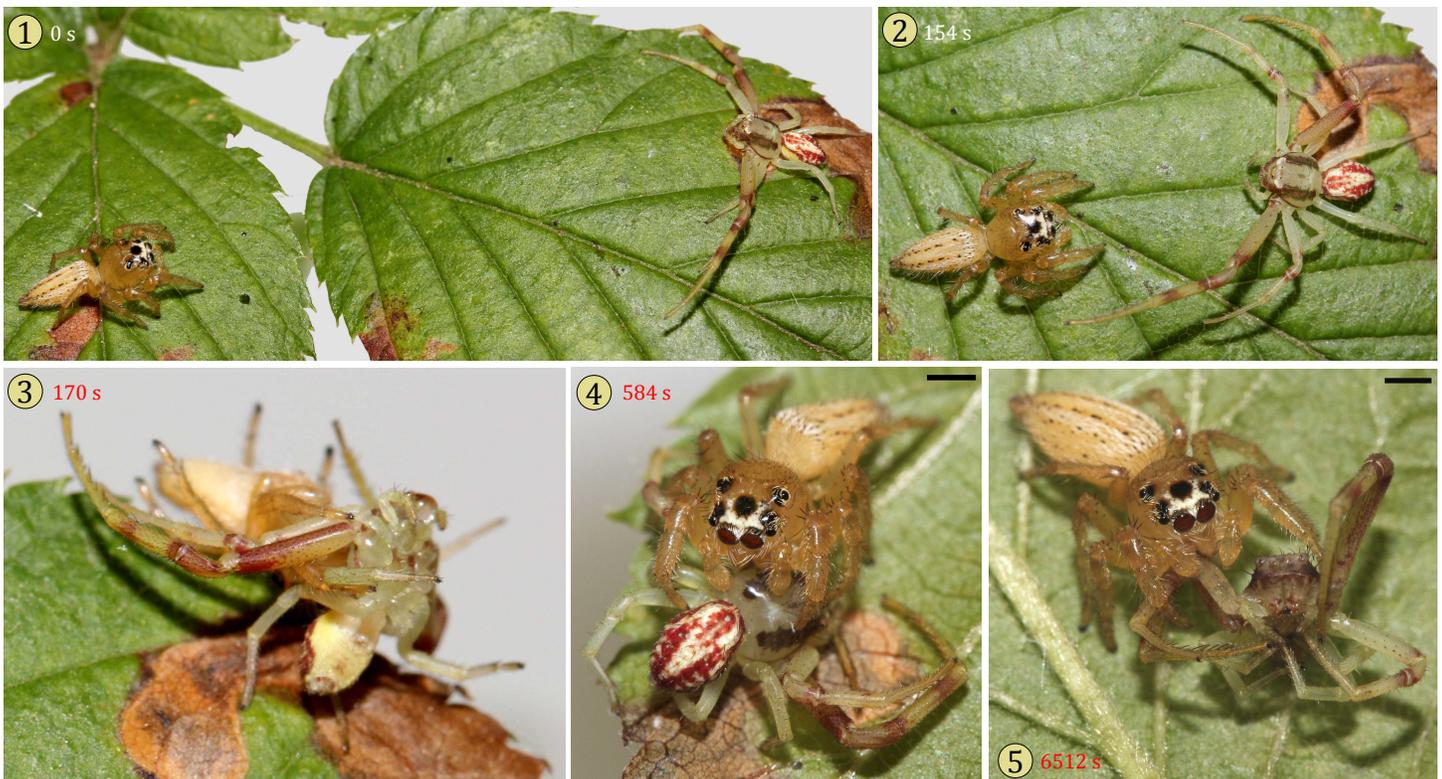


Figure 60. Sequence (1-5) showing the capture of a *Mecaphesa* by a penultimate male *Colonus puerperus*. This *Colonus* walked slowly up to the *Mecaphesa* to a very close jumping position, almost within the reach of legs I and II of its prey (2). 3, The *Colonus* jumped over the front legs of its prey to securely bite its carapace. 5, After macerating the opisthosoma of its prey, the *Colonus* fed through one of its legs.

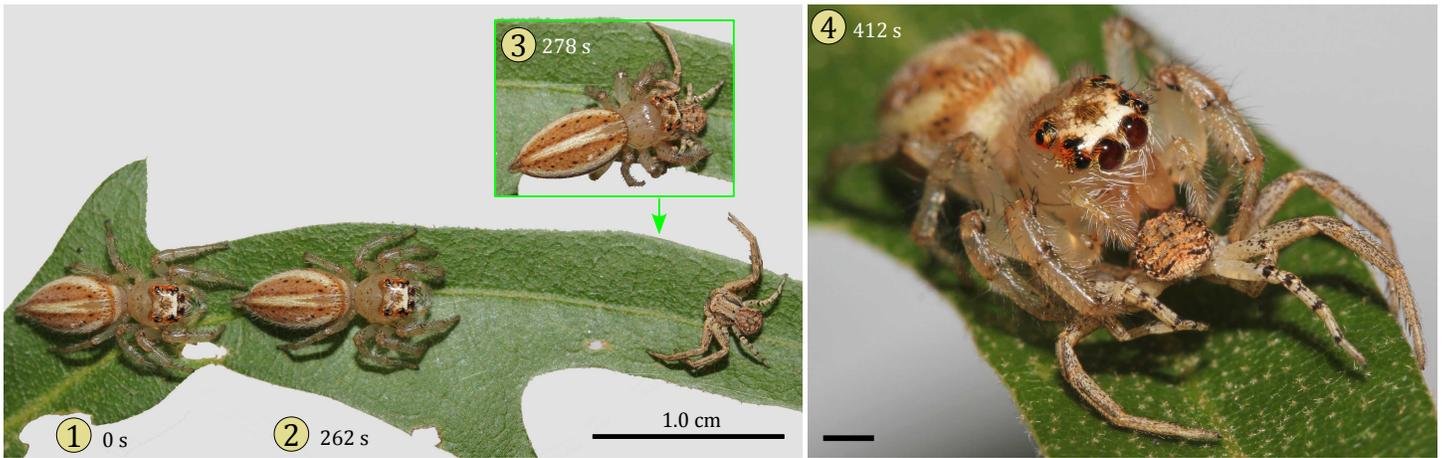


Figure 61. Sequence (1-4) showing the capture of a woodland thomisid by an adult female *Colonus sylvanus*. Note the recoil position (3) immediately after this attack.

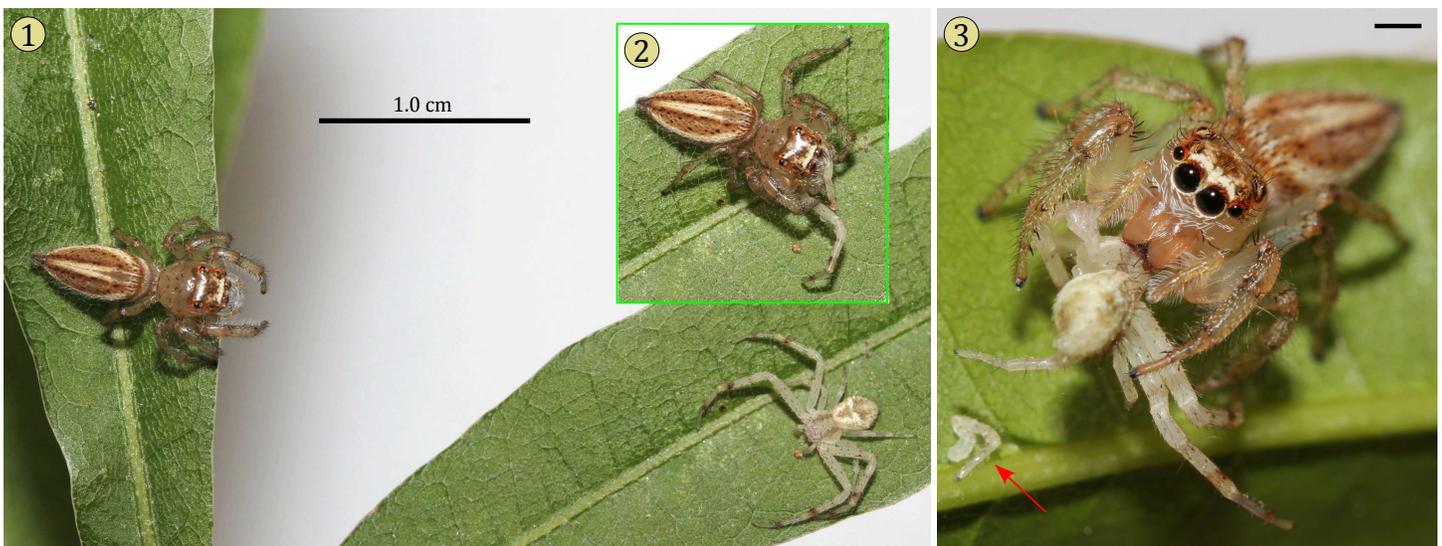


Figure 62. Sequence (1-3) showing the frontal attack of an adult female *Colonus sylvanus* on a thomisid. Note the autonomized limb of this thomisid (arrow, 3).

Prey defenses. The tendency of araneid spiders to hold their spiny legs around the body when resting on or under a leaf can be an effective defense against the attack of a *Colonus* (Figure 63). Otherwise, these spiders are quite vulnerable (Figure 64).



Figure 63. Sequence (1-3) showing the attack of an adult female *Colonus sylvanus* on an araneid spider in a cryptic or defensive position. In this case, any 'crypsis' associated with this position was ineffective. The *Colonus* was not able to attack the carapace of this spider, and came away with only a single autonomized limb, which it fed upon.



Figure 64. Sequence (1-4) showing the attack of an adult female *Colonus sylvanus* on an araneid spider in a vulnerable position. **1**, The araneid spider rested on a leaf, with a single leg extended to hold a silk line. The *Colonus* approached its prey to jump from beneath a nearby leaf (lower left). **2**, Immediately after the attack, the araneid was held securely with a bite to the carapace. **3**, The araneid was pulled off of its leaf as the *Colonus* climbed back to its original position with legs IV. **4**, Later view showing the *Colonus* still holding its prey by the carapace. Note the proximity of tibia LI of the *Colonus* to the femur of L3 of the araneid. As will be discussed in a later section, this position may have something to do with the function of the bulbous setae of *Colonus*.

Relative size is also an important factor in defense. In the example shown here (Figure 65), a larger *Tibellus oblongus* survived the bite of an adult female *Colonus sylvanus*, which subsequently released it. This release may have resulted from the fact this *Colonus* was already satiated, the inability of the *Colonus* to handle the larger spider safely, or from the resistance of the *Tibellus* to the venom of the attacking *Colonus*.



Figure 65. Sequence (1-8) showing the capture and subsequent release of a *Tibellus oblongus* by an adult female *Colonus sylvanus*. **1-3**, Slow advance to the jumping position (**3**). **4**, The *Colonus* jumped over the extended legs of the *Tibellus* to bite it on the rear of its carapace. **5**, The *Colonus* righted itself and held its prey. **6**, Some 5 minutes later, the *Colonus* carried its prey to the edge of the leaf. It is possible that the *Colonus* could detect that this prey was still alive and was moving it to a safer hanging position where the legs of the prey could be less effective. **7**, Note the extended legs of the *Tibellus*, which appeared to revive at this time. **8**, The *Colonus* released its bite but continued to hold its prey over the edge of the leaf until it 'came to life' and quickly scrambled away. The *Tibellus* did suffer a puncture wound to the carapace, but it survived and appeared to be quite normal when I later released it. I have also observed other salticids (*e. g.*, *Phidippus*) dropping prey debris off of the edge of a leaf like this.

Some small spiders, including the araneid *Araneus miniatus* and the thomisid *Synema parvulum* (Figure 66) have some form of protection from the attack of *Colonus*. Both were always rejected when a stalking *Colonus* came into contact with them, and I have not seen any *Colonus* even bite either species. Other araneids and thomisids of the same size were readily taken as prey. The coloration of *S. parvulum* (Figure 66:5) may be aposematic. Many insects, such as the locust borer *Megacyllene robiniae* (Figure 66:6), were observed but never attacked. Although *M. robiniae* is generally thought of as a wasp mimic, the presence of a real wasp would most certainly have aroused a quick flight response by a *Colonus* in the vicinity. As shown previously, thomisids are quite vulnerable to the attack of a *Colonus*, but a larger thomisid that detects a *Colonus* and reacts to it by assuming its own predatory stance (Figure 66:7) may be safe.

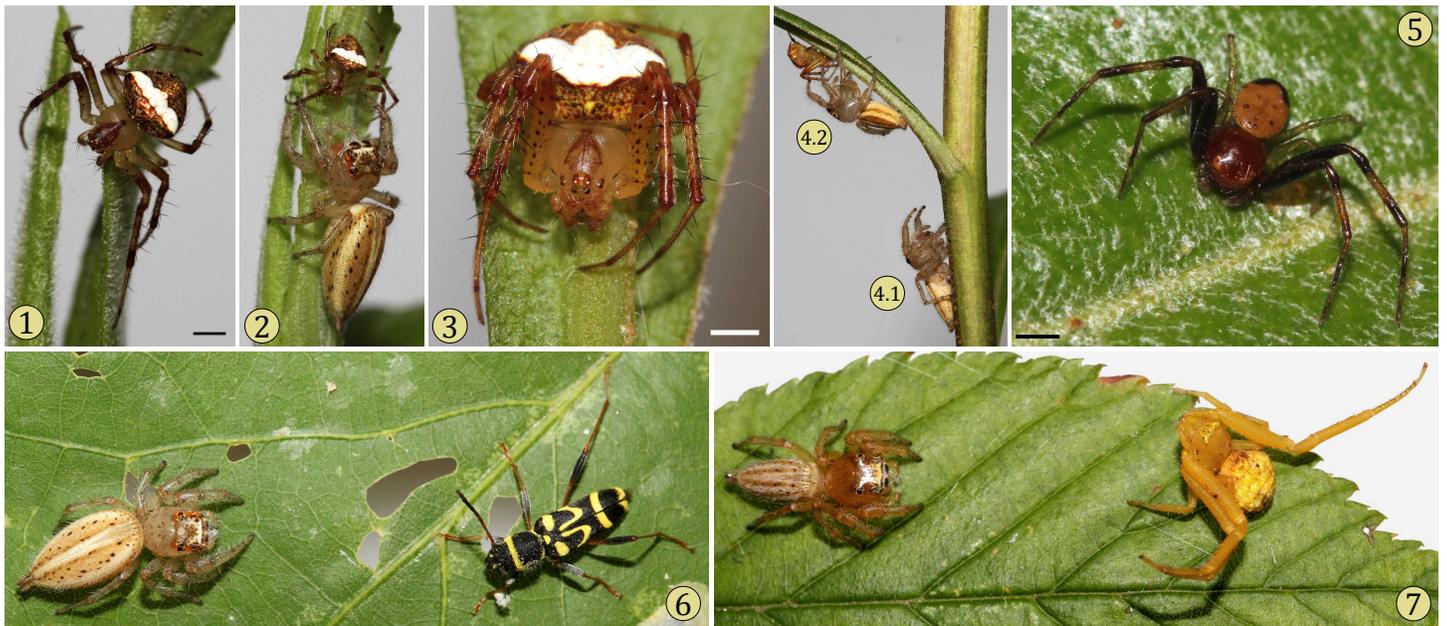


Figure 66. Effective defenses of potential prey animals. **1-2**, This small araneid (*Araneus miniatus*) was stalked from below by an adult female *Colonus sylvanus*, which (2) jumped at it but failed to bite. After this aborted attack, the *Colonus* walked over and around the araneid with impugnty, but never bit it. The defense may have been chemical, visual, or structural. **3**, Another *A. miniatus* resting under a leaf was stalked (4.1) and jumped (4.2) by an adult female *C. sylvanus*, also without a bite. **5**, This small thomisid (*Synema parvulum*) was always dropped by an attacking *Colonus*. It appears to have aposematic coloration and may have a chemical defense. **6**, Observation of a nearby locust borer (*Megacyllene robiniae*) by an adult female *C. sylvanus*, with no attack. The *C. sylvanus* also did not flee from this beetle, thought to be a wasp mimic. **7**, This female *C. puerperus* began to slowly stalk this thomisid at a distance of about 10 cm, but when it approached a 'jumping distance' as shown here, the thomisid reacted to it and assumed its predatory stance. Since this position normally allows the thomisid to capture even a large or powerful bee or wasp, it would have been quite dangerous for the *Colonus* to jump. Instead, the *Colonus* kept its distance, moving around the thomisid while facing it, then turned and slowly walked away. As described previously, *Colonus* would easily attack from the front, jumping over the legs of a thomisid to bite the carapace, if the large legs I and II of the intended prey were not raised in this manner.

Feeding behavior

As they feed, *Colonus* generally macerate the soft parts of their prey and leave the hard parts intact. Feeding on spiders usually proceeds from feeding through the carapace at site of the original bite to maceration of the opisthosoma, and finally to feeding through one or more of the legs (Figures 67-68).



Figure 67. Three stages in feeding on a *Pisaurina mira* by an adult female *Colonus sylvanus*. **1**, Feeding through the original attack site on the carapace. **2**, Macerating the opisthosoma. **3**, Feeding through a leg.

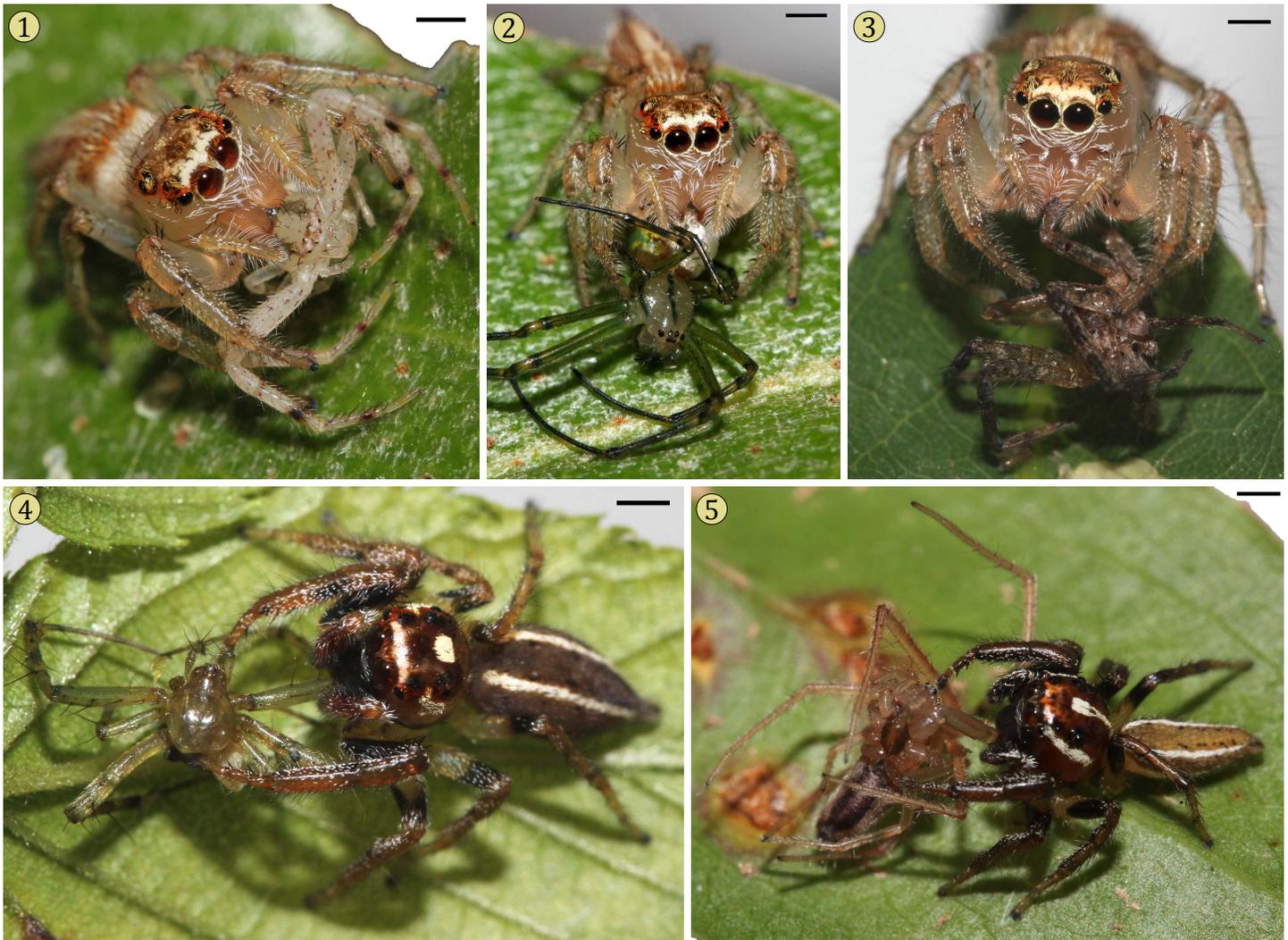


Figure 68. More views of *Colonus* feeding on spiders. **1**, Adult female *C. sylvanus* feeding through the carapace of a thomisid soon after its capture. This represents the usual site of attack with the chelicerae. **2**, Adult female *C. sylvanus* macerating the opisthosoma of a *Leucauge venusta*. **3**, Adult female *C. sylvanus* feeding through the leg of a pisaurid. **4**, Adult male *C. sylvanus* feeding through a leg. **5**, Adult male *C. puerperus* feeding through a leg.

Bulbous setae (*bulbosae*)

In keeping with my earlier effort to establish a latinized name for each category of salticid seta (Hill 2010c), I will refer to the bulbous setae of *Colonus* and related amycines as *bulbosae*. Two pairs of these distinctive setae, each bearing a 'bulbous' base, are found on the underside of tibia I in *Colonus* of both sexes, and all ages beginning with the second instar spiders that emerge from the brood sac (Figures 69-72). The function of these setae is not known (Richman & Vetter 2004), but there is good reason to suspect that they are involved in the handling of prey by *Colonus*, given their situation behind the ventral macrosetae (or spines) of each tibia I.

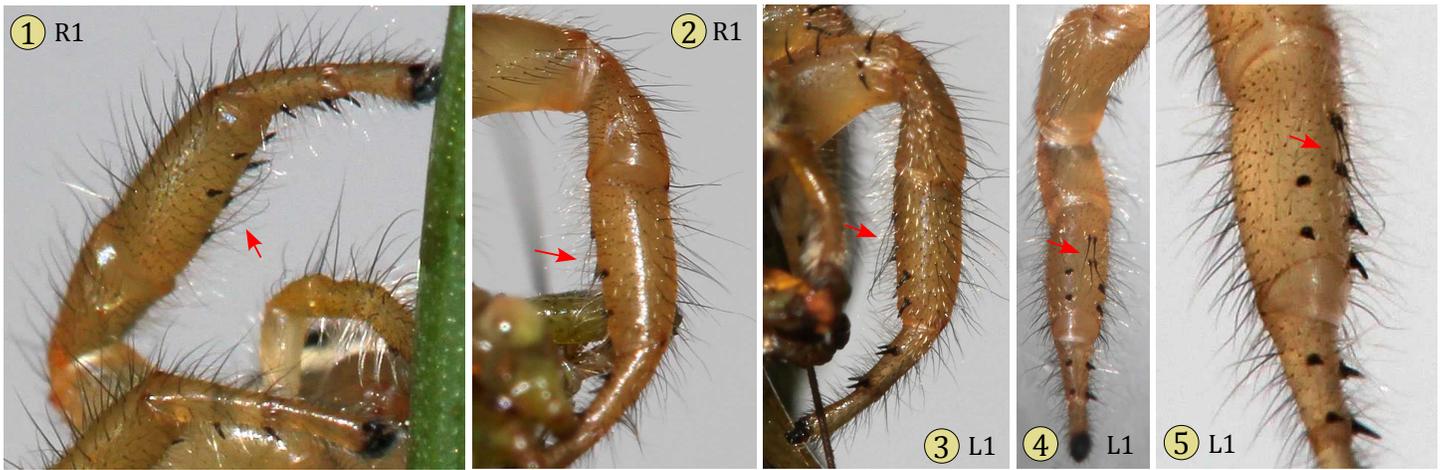


Figure 69. Views of the two pairs of bulbosae (red arrows; 1-2, RI and 3-5, LI) situated antero-ventrally behind the four macrosetae (or ventral spines) of tibia I of living adult female *Colonus puerperus*. **2**, Filaments of the bulbosae appear to contact the leg of the tettigonid field cricket that this *Colonus* was feeding on. The filaments of each bulbosa pair of a *C. puerperus* female appear to diverge more, while those of a *C. sylvanus* are usually parallel and close to each other. Note also the yellowish-brown coloration of *C. puerperus* females.

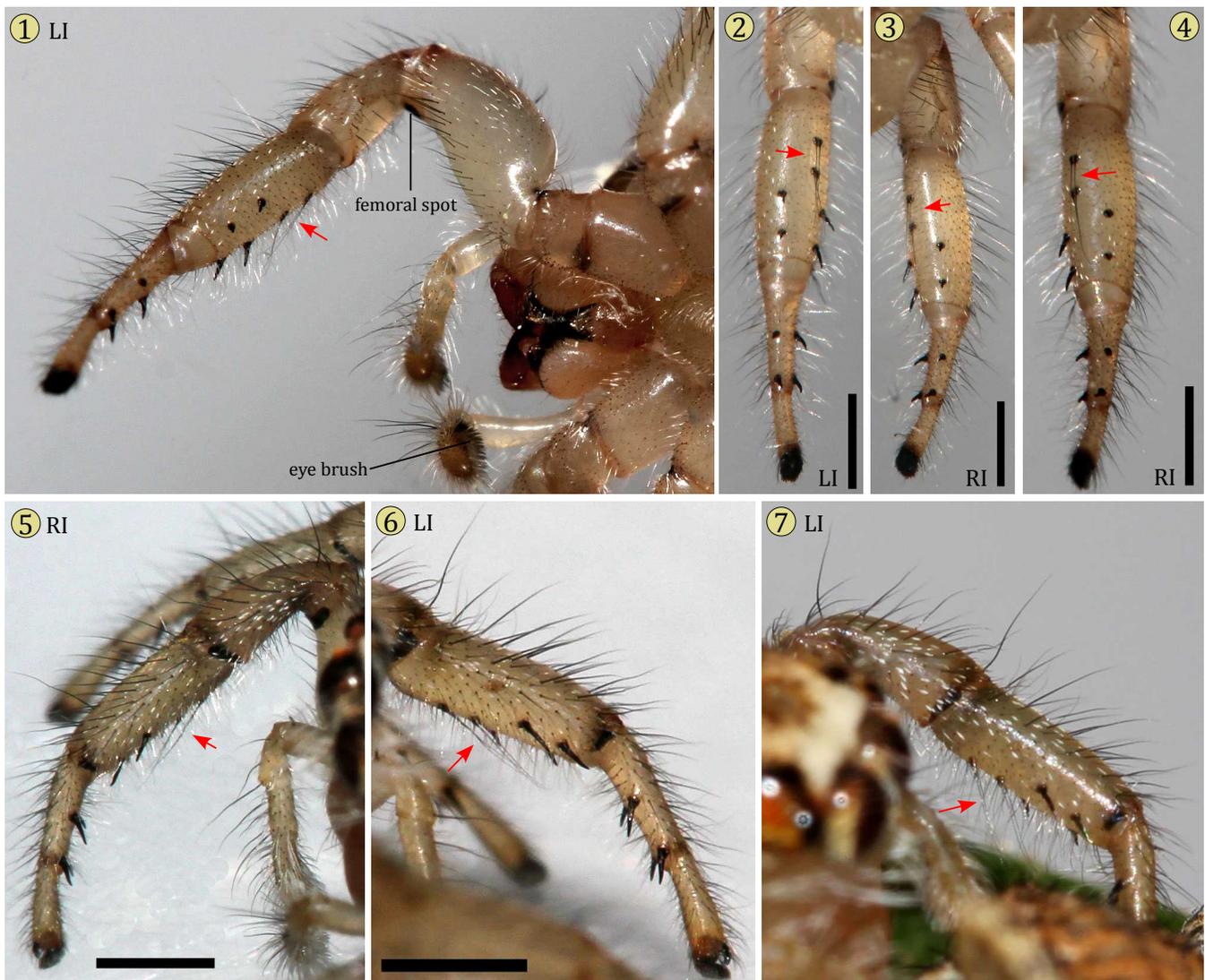


Figure 70. Views of the bulbosae of living adult female *Colonus sylvanus* (red arrows). **1**, Some, but not all, female *C. sylvanus* have black distal femoral spots, as shown here. **2-3**, LI and RI of a different female, ventral view. **5-6**, With backlighting, the retracted claw lever is visible inside of tarsus I. **7**, When holding a newly captured thomisid, the closely parallel filaments of the bulbous setae were directed ventrally toward the prey, at a 40° angle to the tibia.

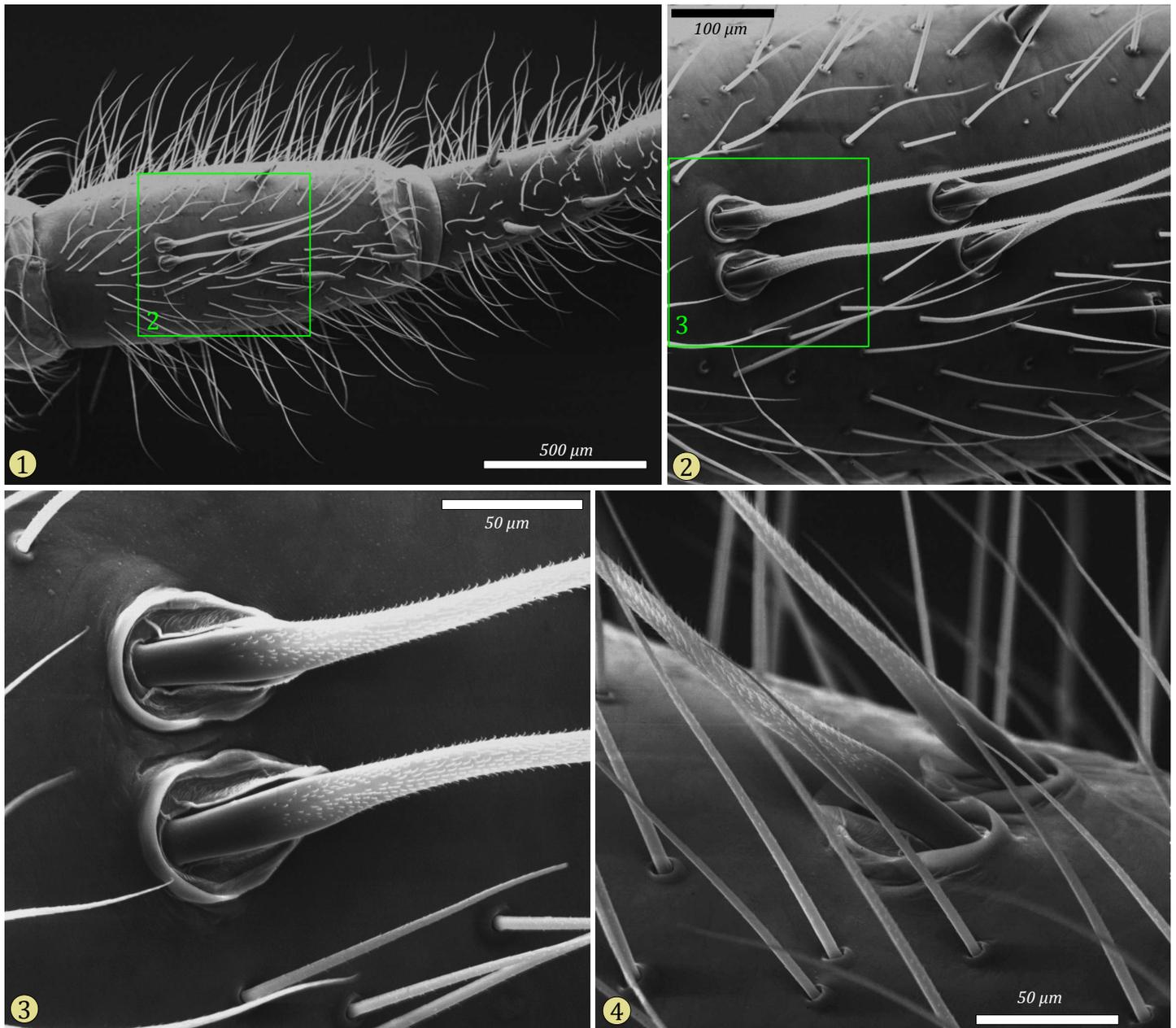


Figure 71. SEM views of the bulbosae associated with RI of an adult male *Colonus puerperus* from Greenville County, South Carolina. **1**, View of ventral aspect of leg, from distal patella (left) to proximal tarsus (right). The inset rectangle shows the area magnified in (2). **2**, The filaments (or setal shafts) associated with each pair of bulbosae are parallel at the base, but, particularly in *C. puerperus*, more divergent distally (1). **3**, Detailed ventral view of the 'bulbs' associated with each bulbosa pair. This basal support structure appears to restrict prolateral or retrolateral movement of these setae, while allowing them to move dorsoventrally in a vertical plane associated with long axis of the tibia. This corresponds to the positions that have been observed in living animals. **4**, Oblique view of a bulbosa pair, at the same magnification as (3). This shows that how the wide bases of the bulbosae are flattened. Their resting position is oriented in a distal direction (to the left in this view), at a 20-30° angle to the long axis of the tibia. No pores that could be associated with chemoreception were observed. Photographs Copyright © Rainer Foelix, used with permission.

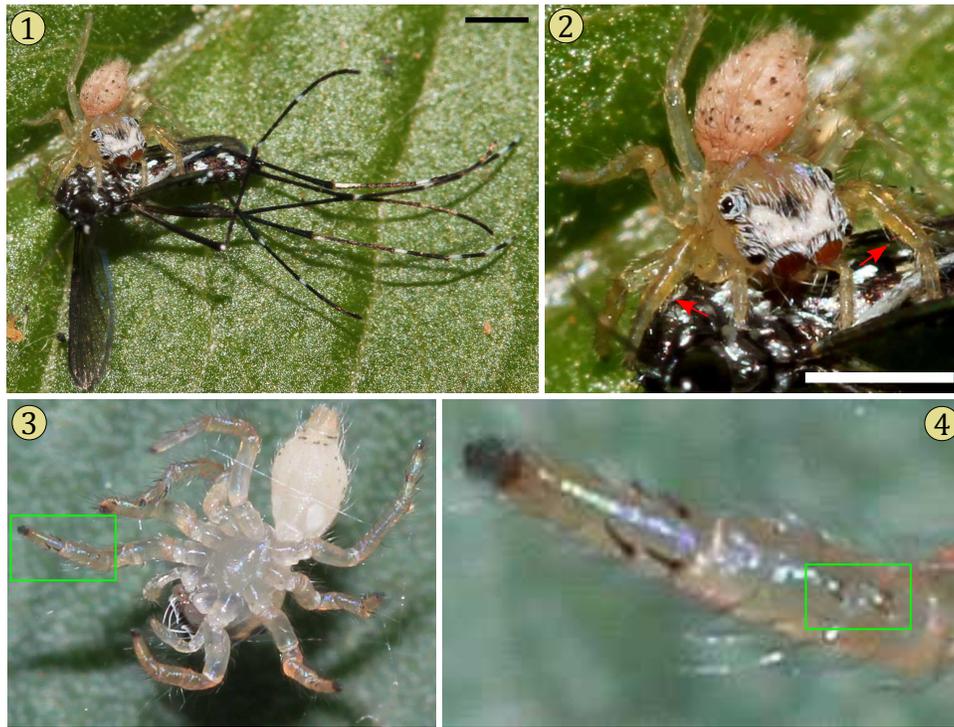


Figure 72. Bulbosae in recently emerged second instar *C. puerperus*. **1**, Holding a culicid nematoceran just after it was captured. **2**, Detail of (1), showing position of tibiae I making ventral contact with the prey (red arrows). **3**, Underside of a spider hanging from silk that it has laid down. **4**, Detailed view of the inset shown in (3), showing the two pairs of bulbosae on the underside of tibia LI (green rectangle). At this stage of development, the four metatarsal macrosetae were already present, but there were none on the tibia.

Colonus generally bring the bulbosae into contact with captured prey, or at least close to that prey (Figures 69:2, 70:7, 72:2, 73-78).

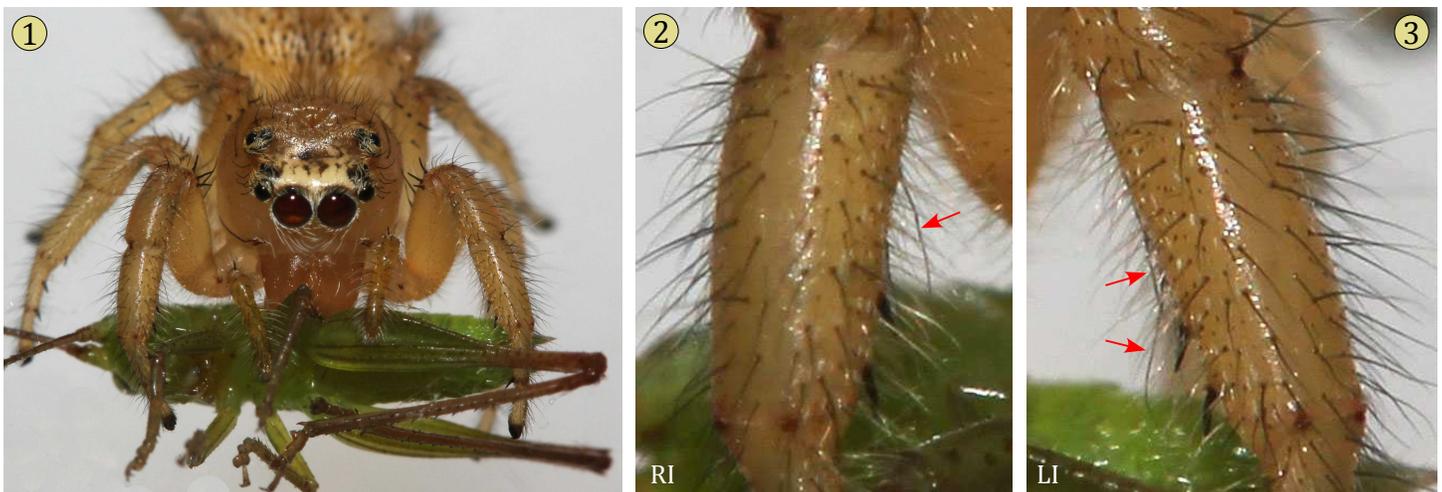


Figure 73. Adult female *Colonus puerperus* holding a tettigonid cricket. Some of the bulbosae associated with RI (2) and LI (3) are identified with red arrows. The ventral to prolateral orientation of these setae supports the hypothesis that they are used to contact prey held with the chelicerae, between legs I.



Figure 74. *Colonus puerperus* holding prey under legs I soon after capture. **1**, Adult male holding a thomisid (*Mecaphesa*) by the carapace. Both legs I of this *Colonus* were resting on the legs of the prey as it was grasped by the chelicerae. **2**, Penultimate female holding a captured acridid grasshopper. **3**, Adult female holding a captured *Mecaphesa* by the carapace. **4**, Penultimate male holding a captured brachyceran fly under tibia RI. **5**, Adult female holding an *Oxyopes salticus*. **6**, Adult female holding a *Tetragnatha*.

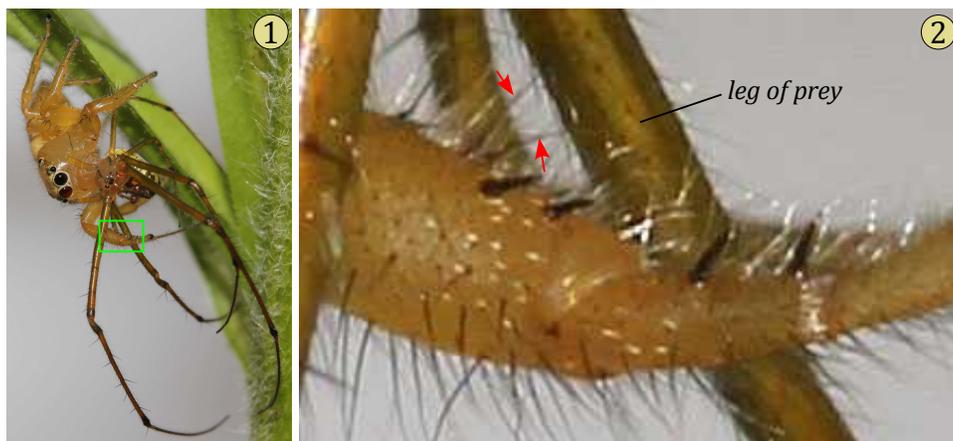


Figure 75. Adult female *C. puerperus* holding a *Tetragnatha* just after its capture with a bite to the carapace. **2**, Magnified view of inset from (1), showing the 'vertical' extension of the flaring (not parallel) anterior bulbosae (red arrows) to contact the leg of this prey.

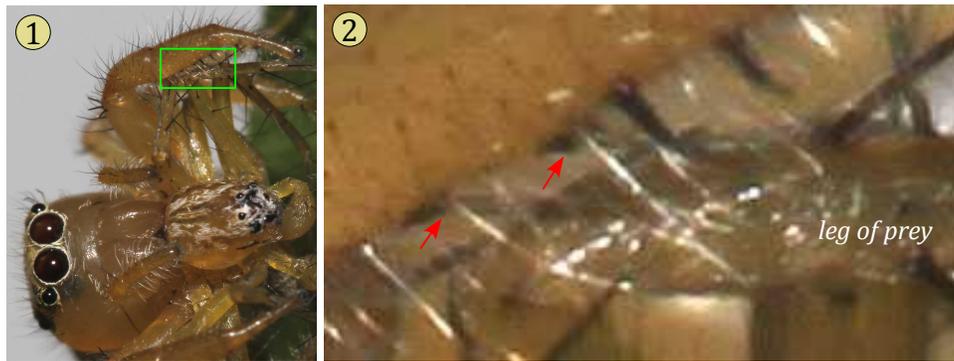


Figure 76. Adult female *C. puerperus* holding an *Oxyopes salticus* just after its capture with a bite to the rear of the carapace. **2**, Magnified view of inset from (1), showing the dark bulbs of the bulbosae (red arrows). Both pairs of bulbosae appeared to be in contact with the leg of this prey.



Figure 77. Adult female *C. puerperus* resting above a *Misumenops*. This *Colonus* approached and walked over the waiting thomisid but did not attack, and was not attacked as the thomisid did not move. Note the extended position of the distal bulbosae of RI (inset rectangle, 2), as they appear to contact setae of the thomisid. It is possible that this thomisid has the ability to conceal vital signs from a *Colonus*.

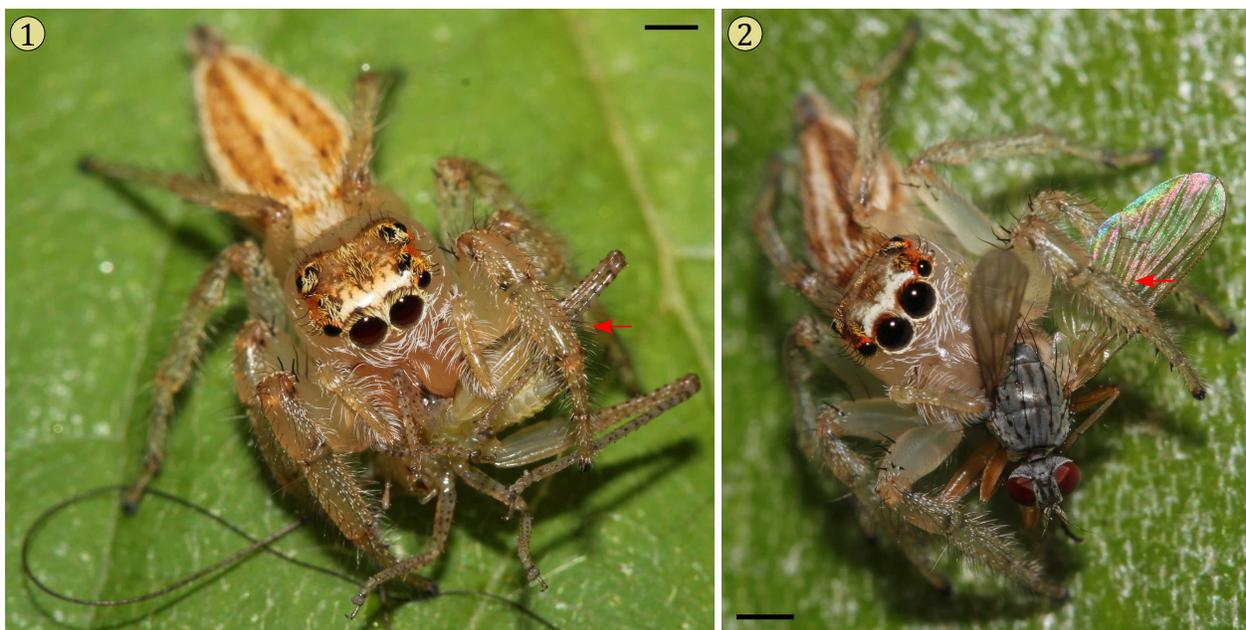


Figure 78. Two different adult female *Colonus sylvanus* holding recently captured prey with tibia LI in close contact with that prey. **1**, Holding a tettigonid cricket. **2**, Holding a brachyceran fly.

Thus one reasonable hypothesis for the function of the bulbosae is the detection of very slight vibrations associated with prey, perhaps the pulse of the heartbeat or transient pressure changes associated with the movement of some setae. Since *Colonus* often prey on immobile arthropods, including dangerous prey like spiders as well as other prey that might feign death, this kind of *vitality indicator* could be useful.

Another hypothesis, also related to their function as a vitality sensor, is that these setae can detect oscillations in electrostatic charge associated with the prey cuticle or setae. The bulbosae certainly look like paired microelectrodes. Structurally, long setae are such good capacitors that they can be difficult to image with SEM. For example, the filaments in Figure 71 are bright white because they have accumulated charge from the electron beam of the microscope. The electrostatic properties of arthropod cuticle have received some study, mostly in Hymenoptera (e.g., Edwards 1962; Warnke 1976; Boucias et al. 1988; Colin et al. 1991; Ishay et al. 1991; McGonigle and Jackson 2002; McGonigle et al. 2002; Galushko et al. 2005; Bush et al. 2008). Cuticle is known to have variable properties of conductance and capacitance. At the size scale of a salticid, electrostatic forces that we disregard can be very significant. To convince yourself of this, try placing an entire exuvium into a small plastic tube! At the scale of the filaments of the bulbosae, electrostatic repulsion of adjacent filaments with like charge might maintain their separation in *C. sylvanus*, where they are usually very close and parallel, even when extended (Figure 70:7). In addition, electrostatic attraction could account for their ventral extension to contact the cuticle of prey. Slight variations or oscillations in the surface charge of prey, associated with electrical activity beneath the cuticle, might be associated with dorsoventral movement of the filaments of the bulbosae.

It is hoped that these hypotheses will encourage further research into a fascinating subject, particularly with our modern interest in microinstrumentation. For reference, observations related to the bulbosae, and their implications are summarized in Table 2.

Table 2. Some observations associated with the bulbosae of *Colonus* and their implications for the function of these setae.

observation	implications
presence of bulbosae in all <i>Colonus</i> and related species	must play an important role in their survival, and they should have behaviors related specifically to their use
presence in males and females of all ages	no sexual function
located behind ventral macrosetae of tibia I, ventral but prolateral	associated with prey contact
no pores in bulbosae	not chemosensory
bulbosa filaments distally oriented and can rotate ventrally to make contact with prey held under tibia I	movement responsive only to vibrations or electrostatic forces directly below the bulbosa, not a wide-angle receptor of air vibrations
either one or both tibia I rests against recently captured prey, even when prey is not tightly held with leg I, but with the chelicerae	suggests that bulbosae are brought into contact with the prey
often a single tibia I is held against prey	reception from both legs is not needed
bulbosae are paired, two bulbosa pairs under each tibia I	improves chance of contact, or stimulus is compared between separated receptors
paired bulbosa filaments of <i>C. puerperus</i> tend to diverge distally, those of <i>C. sylvanus</i> tend to stay parallel and close	close parallel alignment of filament pair is not required for function, but separation may be
even when very close, filaments of paired bulbosae tend to maintain their separation in <i>C. sylvanus</i>	suggests repulsion associated with an electrostatic charge common to both filaments in a pair
<i>Colonus</i> attack immobile prey	could use a vitality sensor to determine if prey is alive
<i>Colonus</i> attack dangerous spiders that often 'freeze' when attacked and then recover	could use a vitality sensor to determine that it is safe to move from the capture position to manipulate and feed on prey
<i>Colonus</i> have not been observed placing their tibiae across silk strands, or against leaf surfaces	probably not a sensor for web vibrations, vibrations on silk lines, or surface vibrations

Grooming behavior

Some of the grooming behavior of *Colonus* that I have observed is documented in Figure 79. Grooming is most readily observed just after a spider has fed. I have previously observed the grooming of the tarsi with the mouthparts and the use of the eyebrush of the the pedipalp to clean the AME in many different salticids. This is the first time that I have observed the *simultaneous* use of a leg and a pedipalp to clean the AME (Figure 79:2), and it is also the first time that I have seen the contact of the eye brushes with the endite brushes (Figure 79:3).



Figure 79. Some of the grooming behavior of *Colonus*. **1**, Adult female *C. puerperus* pulling the tarsus of leg RI through the mouthparts. All four legs are often treated in this manner, pulled between the fangs and the cheliceral bases, and between the brushes of the endites. I have seen this behavior in many salticids. **2**, Same *Colonus* simultaneously brushing the AME with leg RI and the eyebrush of the left pedipalp. **3**, Another adult female *C. puerperus* rubbing the eyebrush of both pedipalps against the laterally separated endite brushes. **4**, Adult male *C. sylvanus* cleaning the right AME with the eyebrush of the right pedipalp.

Use of the feet

The feet of salticids are remarkably versatile when it comes to clinging to surfaces, handling silk, or handling prey. I have previously documented the ability of *Colonus*, and other salticid spiders, to independently extend or retract the footpads or the claws, the role of the footpads in clinging to surfaces, and the role of the claws in the handling of silk (Hill 2007b, 2010c). One point that cannot receive enough emphasis is the versatility or sophistication that these spiders display in applying their feet quickly and effectively to different surfaces and structures as they move (Figure 80), and a great deal remains to be learned about this behavior.



Figure 80. Some of the behavioral versatility displayed by an adult male *Colonus sylvanus* in the use of his feet to cling securely to a leaf. **1**, As it leaned over the edge of a leaf, this male maintained a hold on the edge of the thick central vein of the leaf with the claws of leg LIV (arrow). Salticids, like many other spiders, frequently cling to leaf edges in this manner. **2**, Detail of inset from (I), showing the application of the footpad tenae (tenent setae) to the smooth margin of this leaf.

Claws as talons. The use of the extended claws by *Colonus* to hold prey is shown in Figures 81-82. I have observed this many times, but it is worth recording here as salticid claws are usually associated with the handling of silk lines (Hill 2010c).



Figure 81. Penultimate male *Colonus puerperus* holding a thomisid spider (*Misumenops*). The end of the posterior (retrolateral) claw (2, arrow) RI appeared to be embedded in the cuticle of this prey. Note the extreme degree of extension of the claws and the retraction of the footpads, which are scarcely visible.



Figure 82. Adult female *Colonus puerperus* holding an oxyopid spider (*Oxyopes salticus*) just after its capture. Note the contact of the extended claws of legs RI and LI with legs I of the oxyopid (2, arrows). The bulbosae of RI are also visible, apparently in contact with leg RII of the prey.

Walking on silk lines with the claws. Figure 83 shows an adult female *Colonus sylvanus* walking across two nearly horizontal silk lines in place. Salticids walking across existing lines do not wind them up, but simply traverse them. They appear to locate these lines by waving their legs, and then they grasp them securely with their claws as shown here.

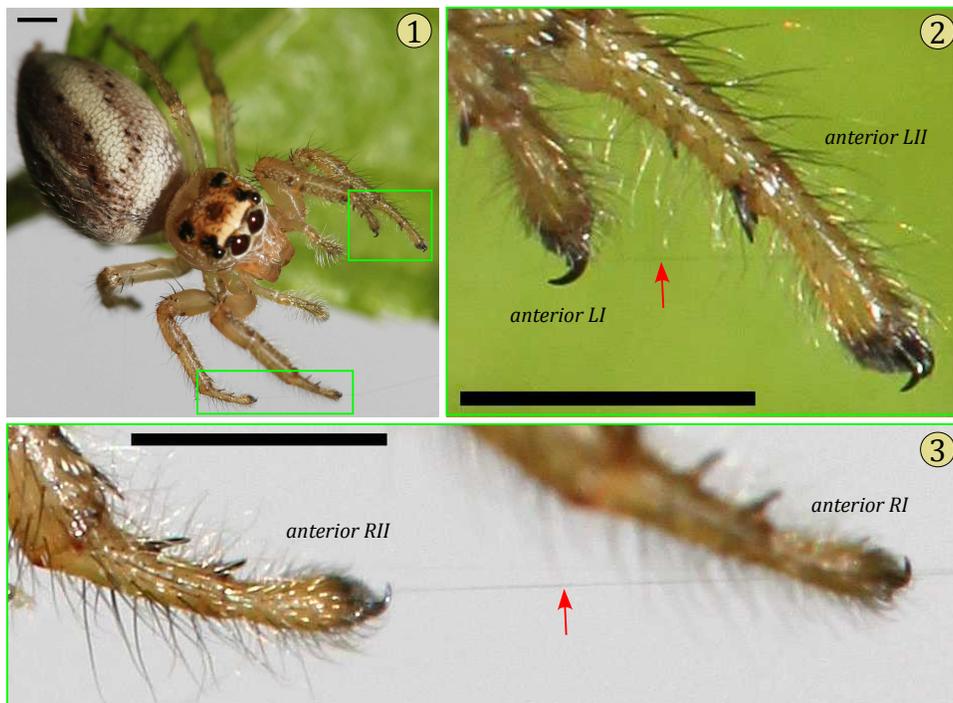


Figure 83. Adult female *Colonus sylvanus* walking on two nearly horizontal silk lines, which can be faintly seen in the detailed views (2-3, arrows). Note the extreme extension of claws of legs I and II, and the retraction of the footpads.

Hanging from a framework of silk lines. A grassland *Colonus* can create a secure resting position by depositing a framework of structural silk (draglines) that it can suspend itself from. In the example shown here (Figure 84), a *C. puerperus* was hanging from a double line with both claws of leg RIV.

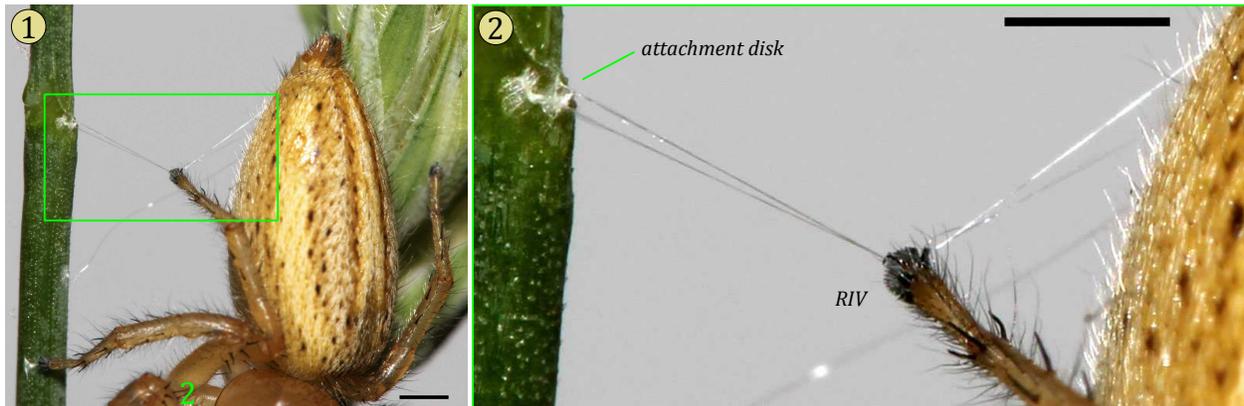


Figure 84. Adult female *Colonus puerperus* hanging from a line that it has placed between a grass stem and flower cluster. The line itself was formed as a two-stranded dragline secured by attachment disks. Note (detail, 2) the use of both claws of leg RIV to hang from this line.

Descent and ascent on the dragline. At times, I have seen *Colonus* rappelling, or descending on a dragline as it was extruded from the spinnerets. I watched one male *C. sylvanus* do this to descend more than 1 m to the forest floor. As do other salticids, *Colonus* can rapidly climb a dragline, collecting the line into a ball as they climb, then discarding this ball by attaching it at the end of their descent. One of the questions that I have attempted to answer in this regard is just how they collect this silk during the ascent. Some of what takes place when a *Colonus* climbs up a line backwards with legs IV is shown here (Figures 85-86).

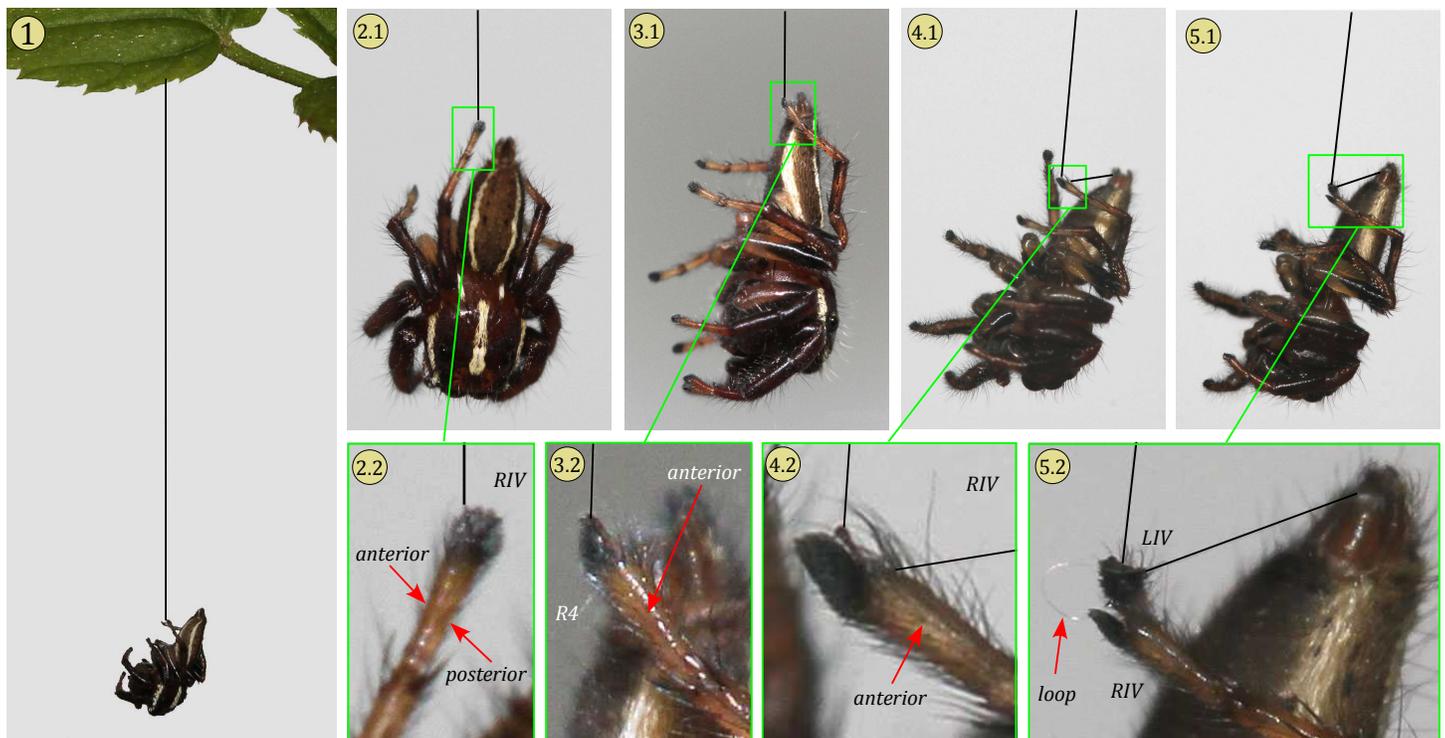


Figure 85. Adult male *Colonus puerperus* hanging from a line. **1**, This male was hanging for several minutes, about 5 cm below a leaf. A black line has been added to show the position of the line. **2-3**, Two views of rotating spider as it held the silk line with the anterior claw of leg RIV. **4**, The spider pulled the line with RIV, raising itself, and reached for the line with LIV. **5**, After releasing the line with RIV, the spider pulled itself up the line with LIV and the resulting slack in the line formed a small loop.

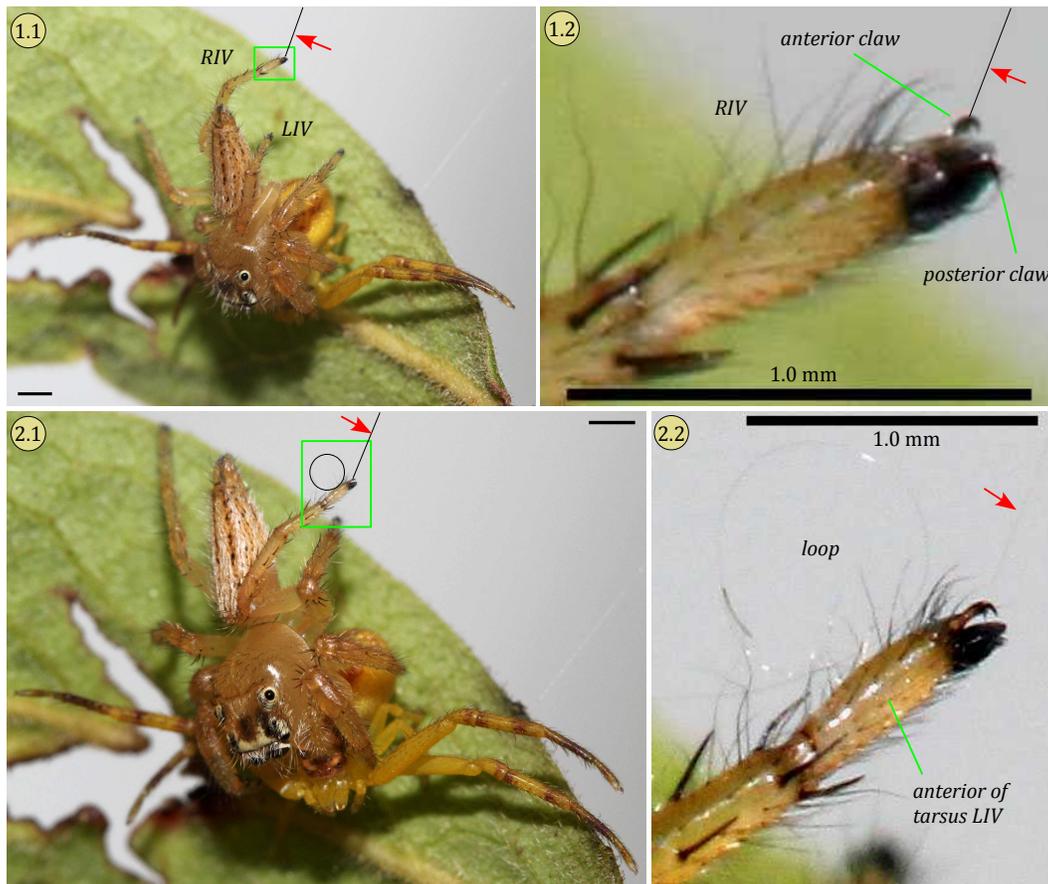


Figure 86. Adult female *Colonus puerperus* holding its dragline after jumping down to capture a thomisid spider (*Misumenops*). For more of this sequence, see Figure 58. **1.1-1.2,** Holding its prey with a bite to the carapace, this *Colonus* held her dragline with the anterior claw of RIV. **2.1-2.2,** The *Colonus* reached up the line with LIV as she moved RIV down to a secure position on the leaf edge. This pull on the line helped to pull the prey off of the surface somewhat, and the resultant slack formed a small loop (detail, 2.2).

The anterior claw of *Colonus*, like that of other salticoids, has tightly spaced teeth that are thought to provide a tight hold on silk lines (Hill 2010c). When salticids turn to rapidly ascend a line with legs I and II, they collect the looped or wound silk mass into a ball which is subsequently discarded by attaching it at the end of the ascent. When holding prey at the end of a jump as shown in Figure 86, however, they will often climb up a line backwards with legs IV, to return to their pre-jump position. As shown in Figures 85 and 86, the small loops in the wound silk that is collected were formed from the slack line associated with each step of the ascent. After each leg IV grasped the line, it pulled on that line to raise the spider, thus creating a small amount of slack in the line between that leg and the spinnerets. With each step, this small amount of slack formed a discrete loop. The *serrula* is a fine comb on the anterior margin of each endite, bearing teeth that resemble those of anterior claw teeth in size and separation. This may assist in the collection of many of these silk loops into a ball during an ascent with legs I and II. Given the ability of these spiders to rotate the endites laterally (Figure 79:3), I suspect that they allow a spider to push its way through a silk fabric, and this may represent their primary function.

Extending the footpads. When a *Colonus* ascends a thin stem, it can secure a good hold on that stem by *isometrically* pushing against it from opposite sides. To do this, the claws can be retracted, and the footpads hyperextended (through eversion of the tenent plates), so that that the tenae (tenent setae) that comprise them spread out in all directions (Figure 87). Based on mechanical models, I have previously (Hill 2010c) developed an explanation or hypothesis for how a salticid, with just a single pulley-like pair of internal cables, can independently control the relative extension or retraction of both claws and footpads.

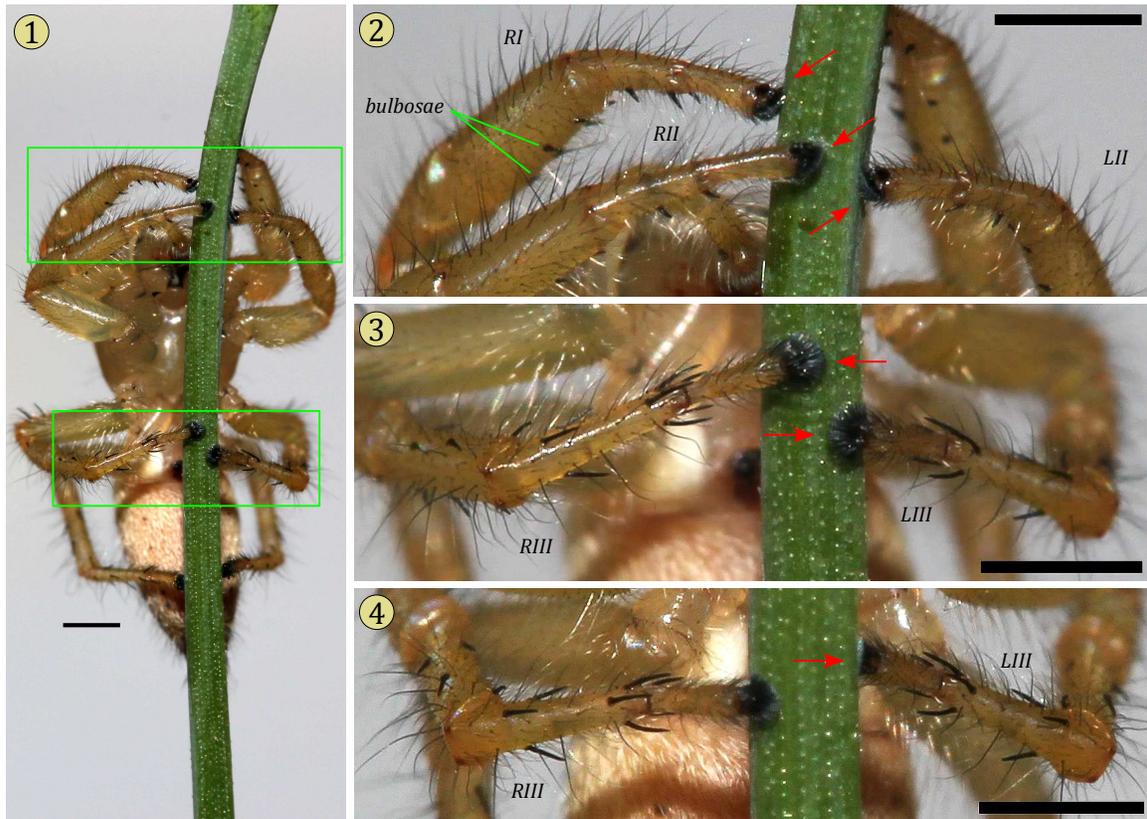


Figure 87. Extension of footpads by an adult female *Colonus puerperus* as it ascended a stem (1). 2, Detail from (1), showing application of the footpads, with claws retracted, to the stem (arrows). 3, Detail from (1), showing extreme expansion and application of the flared tenae of the footpads of legs III to the opposite side of the stem (arrows). 4, Another view of legs III of this spider, showing the iridescent, flattened based of the retracted footpad LIII (arrow). Compare this with the expansion of the same footpad in (3). This iridescence was probably due to diffraction associated with the fine, regular spacing of the adherent tenules on the tenae that comprise this pad.

Anterior medial eyes (AME)

Blest et al. (1988, 1990) found two different patterns of receptor spacing in layer I of the salticine AME. Each *receptor segment* represents the narrow anterior (*distal* or toward the lens) process of a bipolar receptor cell associated with the retina of the AME. In salticines, each receptor segment has a single, long rhabdom within an intracellular matrix that appears to function as a light guide. In the amycoids *Amycus*, *Colonus* and *Scopocira* terminal receptor segments are separated by an unstructured matrix (Figure 88). In many other salticines, including *Phidippus* and *Plexippus*, the receptor segments are contiguous. Curiously, the receptor segments of spartaeines and lyssomanines, each bearing a *pair* of rhabdoms, are also contiguous (Blest et al. 1990).

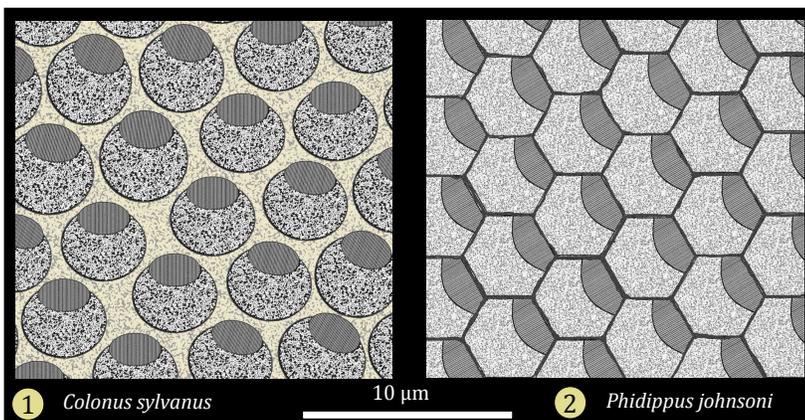


Figure 88. Schematic drawings representing transverse sections of AME layer I foveal receptors for two different salticine salticids (after Blest et al. 1988, 1990). Receptor segments, each with a single rhabdom, are separated by an unstructured matrix (tint) in *Colonus* (1), but contiguous in *Phidippus* (2).

Given the translucent carapace of *Colonus*, it is often possible to see some of the structure of the AME through the lens (Figure 89), as well as some of the movement of the internal eye tubes (Hill 2010a).

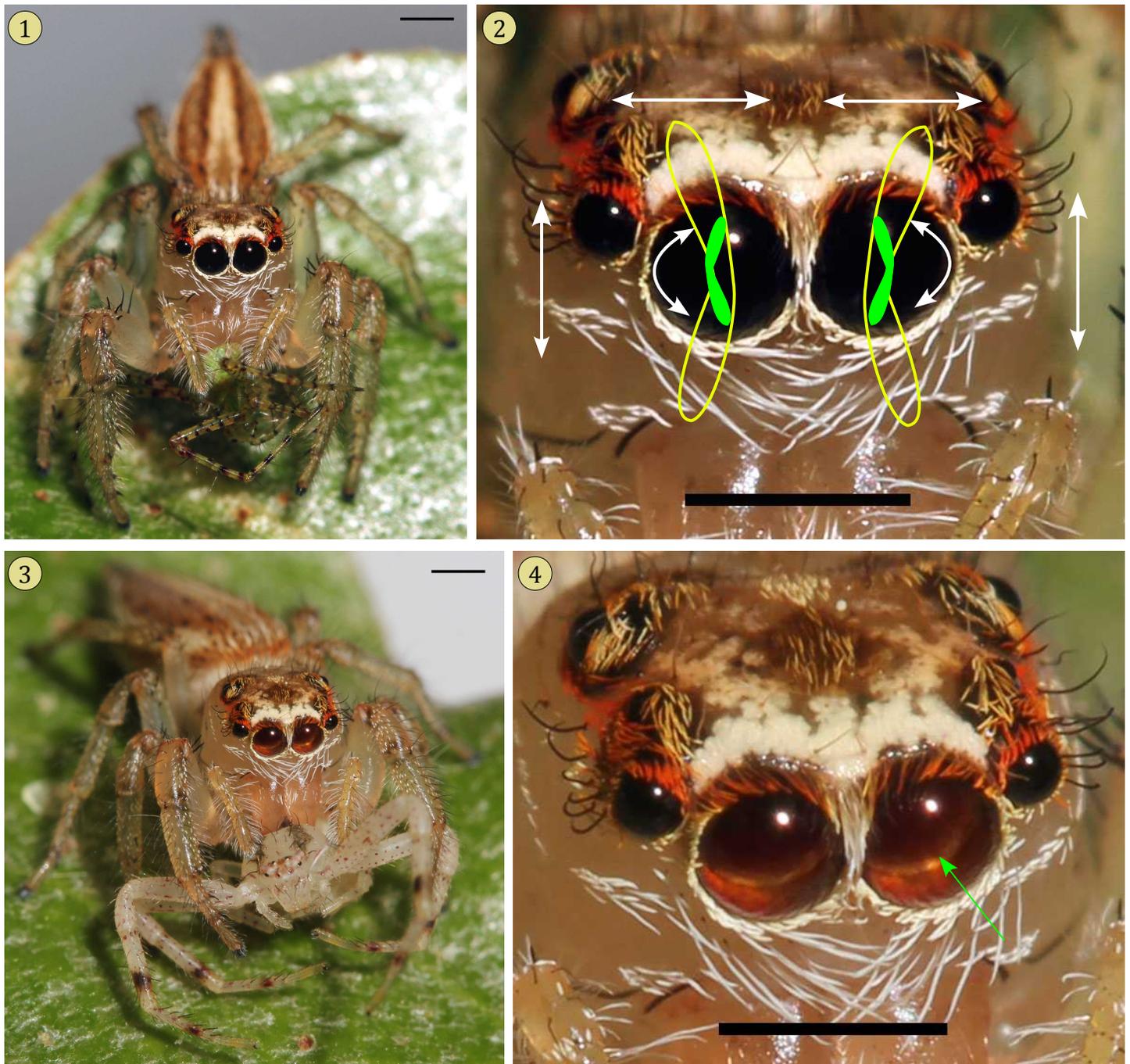


Figure 89. Front view of the anterior medial eyes (AME) of an adult female *Colonus sylvanus*. **1**, Feeding on an immature *Peucetia viridans* (Oxyopidae). When the long tubes of the AME are oriented toward the camera like this they appear completely black. **2**, Detail from (1), with a superimposed projection of the high-resolution, boomerang-shaped layer I of the retinae shown in green. Since the lenses of the AME invert the image, a projection of the field of vision of these retinae directly in front of the spider (yellow outline) is likewise inverted. Arrows have been added to emphasize the fact that each retina can move horizontally and vertically, and can be rotated in either direction (Land 1969a, 1969b). **3**, Feeding on a thomisid spider. In this view, where the AME tubes are not oriented directly toward the camera, it is possible to observe some of the structure of the lens through the AME. Thomisids also scan with their small AME (personal observation), but these have relatively few receptors (Corronca & Terán 2000). **4**, Detail from (3), showing (arrow) the boundary between the rigid corneal lens and the flexible eye tube of smaller diameter behind it. The angle of the flash was almost normal to the plane of these photographs.

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