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Author: William G. Eberhard

Source: *Arachnology*, 17(9) : 485-490

Published By: British Arachnological Society

URL: <https://doi.org/10.13156/arac.2018.17.9.485>

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## The webs of *Neoantistea riparia* (Araneae: Hahniidae): are dew drops helpful in prey capture?

William G. Eberhard

Smithsonian Tropical Research Institute,  
Universidad de Costa Rica,  
and  
Museum of Natural Sciences,  
Louisiana State University,  
Baton Rouge, LA, USA  
email: william.eberhard@gmail.com

### Abstract

The webs of hahniid spiders are poorly known. Those of *Neoantistea riparia* (Keyserling, 1887) all included sheets near the surface of the ground, but were more complex and variable than the simple sheets mentioned in previous accounts. Additional components included: sparse tangles of variable size above the sheet; lines below the sheet; small, dense tangles near some edges of the sheet; and a temporary feeding chamber below the sheet built near a recently captured prey. Webs were close to the surface of damp ground and, as a result, spent long periods coated with droplets of water. These droplets may aid in prey capture, as water accumulated on struggling prey and may have hindered their escape. In contrast, droplets seldom adhered to the spiders.

**Keywords:** Louisiana • sheet web • tangle web

### Introduction

Hahniidae is small, poorly studied family of approximately 23 genera and 346 species (World Spider Catalog 2018). Phylogenetic analyses have placed it near the funnel-web family Agelenidae (Garrison *et al.* 2016; Fernández *et al.* 2018). These small spiders have been commonly described as building sheet webs at damp sites near the surface of the ground (Emerton 1902; Nielsen 1932; Kaston 1948; Comstock 1967; Opell & Beatty 1976; Roberts 1996; Kunt, Yağmur & Ulgezer 2008). The webs of *Antistea* and *Hahnia* (Roberts 1996), and also *Neoantistea* (Opell & Beatty 1976) are thought to lack retreats. Bristowe (1939) believed that *Hahnia helveola* preyed especially on ants, while Forster & Forster (1999) mentioned collembolans as probable prey for New Zealand species.

Hahniid webs are often noticed when they are loaded with numerous tiny water droplets that glint in the sunlight (Shinkai & Takano 1984 on *Hahnia corticola*; Forster & Forster 1999 on several New Zealand species; Kunt, Yağmur & Ulgezer 2008 on *Antistea elegans*) (Fig. 1C). In contrast with the webs of agelenids, hahniid webs that lack water droplets are nearly or completely invisible to the naked eye (Kaston 1948; Opell & Beatty 1976; Kunt, Yağmur & Ulgezer 2008), and it is likely that most (if not all) published descriptions of hahniid webs are, in fact, descriptions of the distributions of droplets. The droplets can obscure, however, details of web structure.

This note describes details of the webs and attack behaviour of *Neoantistea riparia* (Keyserling, 1887). It suggests that web designs are more diverse than previously

appreciated, and that the water droplets have a previously unsuspected significance in prey capture. The question of whether the water condensation is simply an incidental consequence imposed by the physically challenging environment near the surface of damp ground, or is a previously unappreciated aid in prey capture by web spiders has apparently never been posed.

### Methods

The study site was the Lake Ramsay Savanna Preserve near Covington, LA, USA, in an open area (Fig. 1A) with boggy patches where winged pitcher plants (*Sarracina alata*) grew. Observations were made in April of 2018, about 4–5 weeks following a routine maintenance burn. The grass was only beginning to regenerate (Fig. 1A–B), making it unusually easy to see webs near the ground. Much of the ground surface was visible, and there were up to 20 webs/m<sup>2</sup> in some places (Fig. 1B). I located webs by using the glint of sunlight on the droplets (Figs. 1C, 2A). Web sites were marked individually in two quadrats > 50 m apart where they were common and there were no nearby trees, using pieces of masking tape stuck to twigs that were inserted into the ground near webs (Fig. 1B). These web sites were then revisited six more times at approximately hourly intervals to check for the presence of water droplets, from 9:45 am to 4:00 pm (Central Daylight Savings time) on 11 April, a warm, cloudless day (the maximum temperature was 25°C at about 2:00 pm in nearby Covington, LA). All the marked web sites were in full sunlight that was broken only by small patches of shade from nearby tussocks and grass blades, except at the final visit at 4:00 when shade from trees fell on one of the two plots. Chunks of soil with webs of small individuals were placed in closed containers and brought into the lab to observe webs and behavior under a dissecting microscope.

Prey retention was observed in the field by dropping worker *Solenopsis invicta* ants (a recent invader species in the southern US) onto open areas of droplet-covered webs of mature spiders, and measured by the time elapsed before the ant escaped from the web or until >120 s had passed. All ants struggled vigorously and continuously. Attack behavior was observed in captivity under a dissecting microscope by dropping small flies onto open areas of the webs of immature individuals. Setae and the cuticle surface of an exuvium of a nymph were observed in a scanning electron microscope (SEM).

By marking web sites in the morning of a second, warmer day (25 April; maximum 26.7°C in Covington) and then revisiting them late in the afternoon when their dew drops had dried off, web structure was documented by photographing webs after they were lightly powdered with talcum powder.

I use the term “sheet” loosely in the descriptions below, despite the fact that the webs were to some extent three dimensional; the word “tangle” indicates a three-dimensional array of lines that lacked obvious organization. Brent Opell kindly identified the species. A voucher specimen has been deposited in the Museo de Zoología of the Escuela de Biología of the Universidad de Costa Rica.



Fig. 1: **A** general view of the recently burned area of pine savanna habitat where observations were made; webs were studied in open areas similar to that in the middle foreground (the object in the near foreground is a *Solenopsis invicta* ant nest); **B** portion of one of the two small quadrats where web sites were marked and the water droplets on webs were then checked periodically throughout the day (arrows indicate three of the tape labels; the tape is 1.9 cm wide); **C** typical large web built on bare ground seen from above, with the water droplets glinting in the sunlight (the web is about 10 cm from top to bottom in the photo; the dotted line indicates the web's approximate extension).

## Results

All webs that I found coated with water droplets were less than 1 cm above the ground surface. They occurred at sites where the soil was soft and muddy (where my knees made an impression of 2 cm or more and became wet when I knelt there). None were seen higher above the ground at these sites, at sites where the soil was drier and firmer, or where puddles of water stood in depressions. Once the droplets had evaporated, even the densest portions of the webs of the largest spiders were invisible, so I was not certain whether webs also occurred in the drier sub-habitats where droplets would not have formed.

The webs had variable, irregular outlines (Fig. 1C), and were as low as only 1–2 mm above the soil surface. Typically, several objects such as grass stems projected through the sheet, and the sheet seemed to slope upward near these objects as well as at some edges (Fig. 2A–C); similar upward-sloping pimples, where stems projected through the sheet, also occurred in the agelenid *Agelena labyrinthica* (Nielsen 1931). The fact that the droplets glinted simultaneously in the sunlight as I moved my head (and thus changed the angle from which I viewed them) gave the illusion (due to their spherical shapes) that the webs were planar. In fact, close-up photos taken from above showed that some droplets partially obscured others (Fig. 2C), so the lines on which the droplets rested were not all in the same plane. Freshly built webs of three immature individuals in captivity also had some lines with droplets above the sheet when they were

observed under a dissecting microscope (Fig. 4A). Spiders in captivity extended the areas of their webs from one day to the next. Some webs in the field sagged into contact with the ground, at least later in the day (Fig. 4B).

The spider lurked under a larger object such as a grass stem at the web's edge or in the midst of the sheet, or under the sheet itself (in contrast with *Hahnia* spp. and *Antistea elegans* which rested on their sheets: Bristowe 1940). When disturbed, the spiders moved away from the sheet, into the surrounding stems and soil where they were very difficult to see.

Of the 21 *S. invicta* ants dropped onto webs, 12 fell onto the apparent sheet covered with droplets, while the other nine were retained and struggled in invisible lines above the droplet-laden lines. Of those encountering droplets, nine immediately began to accumulate larger drops of water on their bodies as they struggled (Fig. 3); the large drops appeared to impede the ants' mobility.

Details of a total of 13 ant escapes were observed: three occurred when the web sagged or broke under the weight of the ant and its water droplets, and the ant came into contact with the ground below and pulled free as its own water droplet flowed away onto the ground; nine escapes occurred when the ant contacted and crawled onto an object at the web's edge; and one occurred when the ant contacted and climbed onto a stem that projected through the sheet. None of the ants were accepted as prey; the spider ran across the web's upper surface to approach the ant, and then ran directly back to its retreat.

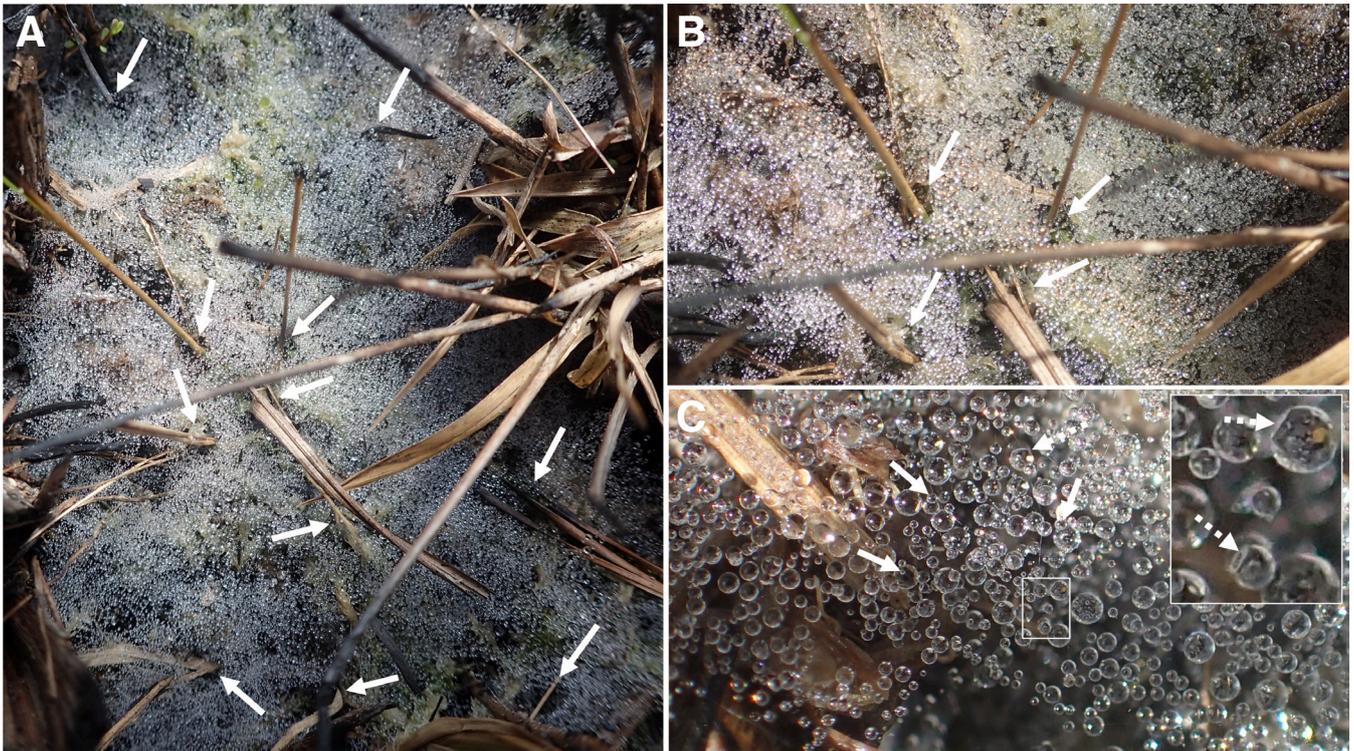


Fig. 2: **A** typically droplet-laden web of an adult built at ground level (seen from above) had multiple plant stems and grass blades projecting through the sheet (arrows) (the photo is about 8.5 cm from top to bottom); **B** objects projecting through the web were often surrounded by small free spaces (arrows); photos of powdered webs (e.g. Figs. 3B, 4D–E) suggested that there were web lines in these spaces, but they were not loaded with droplets; **C** close-up image shows how some droplets on an apparent “sheet” (seen from above and slightly to the side) were not all in the same plane, as some droplets overlapped others (some are indicated with solid arrows). Probably most droplets rested above the web lines, but a few were flat on one side (dotted arrows in the more highly magnified inset), suggesting that they were alongside web lines.

All of the 25 droplet-covered webs whose sites were marked before 9:45 am still had dense accumulations of droplets at 12:30 pm. The first obvious reduction in droplet density was noted in three webs during the next round of observations at 1:54 pm. The droplets had largely or completely disappeared from 15 webs at the final check at 4:00 pm.

When I powdered webs from which droplets had largely or completely disappeared, several impressions from droplet laden webs were confirmed, and further details were revealed. All webs had a well-defined, densely meshed horizontal sheet that sloped upward at the edges where it was attached to surrounding objects, and where stems or other objects protruded through the sheet (Fig. 4B–E). The lines in the sheet were so dense in some portions that individual lines could not be distinguished (Fig. 3B,C,F), but they were sparser in others, especially near objects protruding through the sheet (Figs. 3D, 4D). I did not discern any other consistent patterns in the lines in the sheets.

There were sparse lines above portions of some sheets, but large portions of all sheets had no lines above them (Figs. 3B,E,F, 4A,C); some had a small tangle of lines at one edge of the sheet (Fig. 4E). A few had a small, independent sub-sheet that merged with the larger sheet at one edge (Fig. 4C). In several webs, a portion of a sheet that had been covered with droplets earlier in the day apparently sagged subsequently onto the ground below (Fig. 4B). In several other webs, a dense accumulation of droplets was visible sparkling in the space under the sheet (Fig. 3C), indicating that there were many additional lines below the sheet. In

only one web was there a suggestion of a tubular retreat at the edge of a sheet.

I observed in better detail under a dissecting microscope six attacks and aborted attacks by immature spiders on flies (*Drosophila* sp. and a phorid) that I dropped onto sheets (which had only small water droplets, e.g. Fig. 4A). All six flies also accumulated at least one ball of water as they moved; in contrast, the spiders accumulated little or no water; in only two cases did the spider briefly carry small droplets of water despite having contacted drops on the web (in one of these cases a droplet came off on the spider's chelicerae when it bit a water-covered fly).

One spider with a large fly made several excursions to the ground below and built an oval chamber, then broke some of the lines attached to the fly by pulling the line to its mouth with an anterior leg and then releasing the broken end from its tarsus without any apparent tugging. The spider eventually pulled the fly down into the chamber, where it began to feed. The next day the fly's shrunken body was in the same place (Fig. 4A), but the spider was gone. In none of the spider's apparent spinning activities did it grasp lines with its hind legs or bring them to the spinnerets with a leg to make an attachment, as occurred in a sheet-building lycosid (Eberhard & Hazzi 2016) and as is typical of araneoid and deinopoid species (Eberhard 1982; Coddington 1986). Mostly the spiders were on top of the lines on which it walked, but they also walked readily upside-down below lines.

Tiny droplets of water formed on the setae of an immature *N. riparia* that was placed in a humid environment after being cooled in a refrigerator, suggesting that the setae are

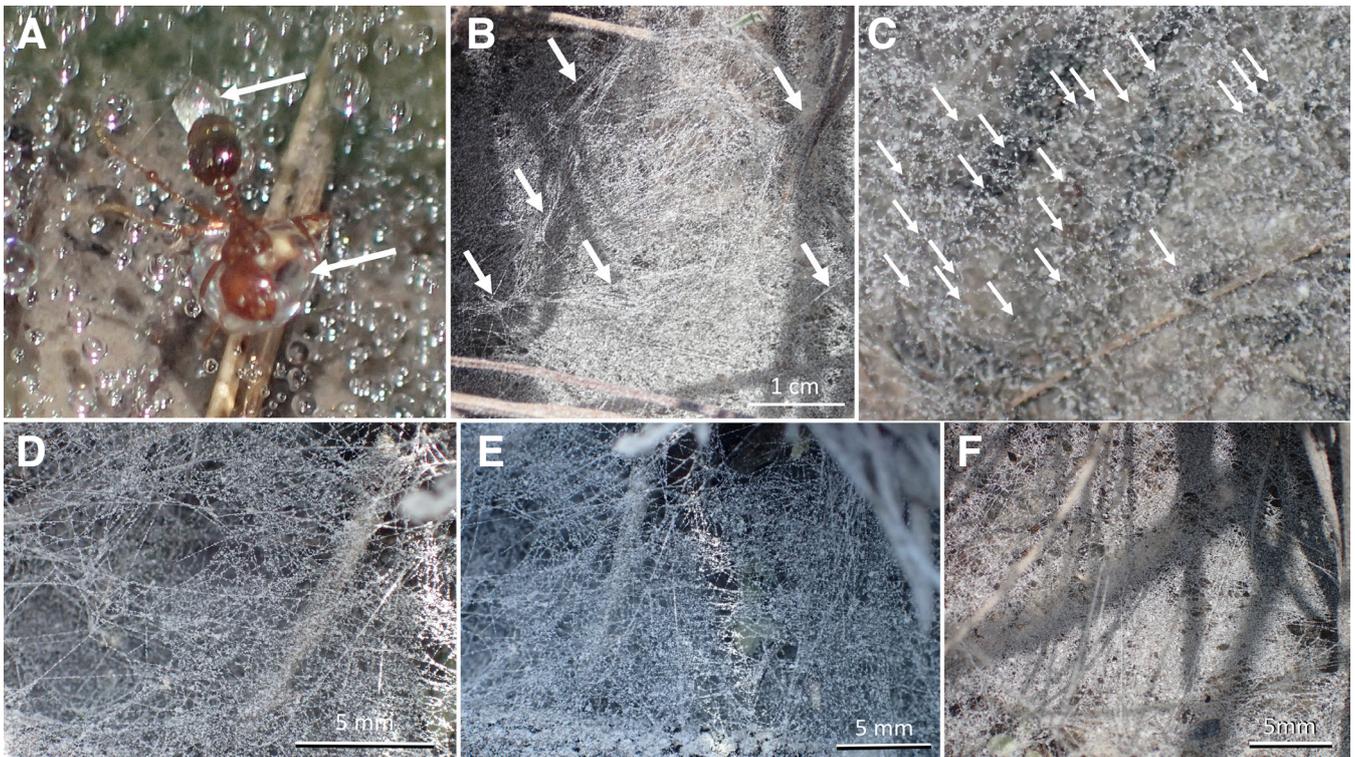


Fig. 3: **A** two large drops of water (arrows) accumulated on the body of a *Solenopsis invicta* ant (about 2 mm long) as it struggled on a droplet-laden sheet of *N. agilis*; **B** multiple tangle lines (arrows) above the sheet of this powdered web, especially on the left side where they were attached to a grass blade that protruded through the sheet; **C** water droplets (some indicated by arrows) below this powdered sheet, from whose upper surface the water droplets had evaporated; **D** close-up photos showed that the density of the lines varied, and that they had no obvious organization; **E** in a few places, the orientations of lines seemed to be consistent (note the many lines that appear horizontal in this photo); **F** lines were so dense in some areas of some sheets that individual lines could not be distinguished (it is uncertain whether the small holes in this sheet were produced by damage from falling objects). All photographs were taken looking down from above.

hydrophobic. The cuticular surface of the legs was relatively smooth (Fig. 5), with no obvious modifications to repel water, such as those in some other arthropods such as collembola (Wolff *et al.* 2014, 2016).

## Discussion

All webs of *N. riparia* included sheets on or very near the surface of the ground, as described for other hahniids. Additional lines were also often present, however. They included long, isolated lines or very sparse tangles just above the sheet (Figs. 3B, 4D), dense tangles at more protected edges of sheets (Fig. 4A,E), retreats at the edges of or below sheets, and lines below the sheet (Fig. 3C). Previous characterizations of the other hahniid webs as “sheets” may thus have been overly simplified. Two differences from the designs of typical funnel webs of agelenids were the lack of any clear tube connected with the sheet, and their invisibility. Other behavioural details that were similar to agelenids include running rapidly on the lower as well as the upper surface of the sheet (Nielsen 1931 on *Tegenaria derhami*) (also reported for *N. agilis* by Opell & Beatty 1976), and easily cutting web lines (Nielsen 1931 on a mature male *A. labyrinthica*). The fact that *N. riparia* webs lasted several days in captivity and were gradually extended by the spider means that it was not certain whether the webs observed in the field were the result of one or more nights of construction activity.

The accumulation of water droplets on the webs of *N. riparia* (and other species with webs near the ground) is likely due to physical processes in which the silk lines act as nuclei on which droplets of water condense from over-saturated humid air whose temperature is lowered near the cool surface of the ground. When the ground is cooler than the air just above it, the air temperature in the boundary layer at the ground surface can be sharply lower than that of the air farther above the surface, due to the reduced eddy diffusion in the boundary layer in the first few mm above the soil (Geiger 1950). The observations here indicate that water droplets are probably present during a substantial fraction of the functional lifetime of the webs of *N. riparia* in the field. Webs bore droplets for surprisingly long times, even on a warm, sunny day with very little shade in an open field from which most sheltering ground cover had been eliminated. Presumably, even longer durations would occur on cooler, cloudier days, and at more sheltered sites. Dense arrays of water droplets also occur on the sheets and tangles of erigonine linyphiids built next to the ground (Emerton 1902; Nielsen 1931; Forster & Forster 1999).

The water droplets may significantly increase the prey capture properties of *N. riparia* webs. Vigorously struggling prey in webs bearing numerous water droplets often accumulated large drops of water on their bodies (Fig. 3A), and these drops appeared to constrain their movements. Further observations of escapes by other prey, and from similar webs without droplets will be needed to evaluate the biological significance of these observations.

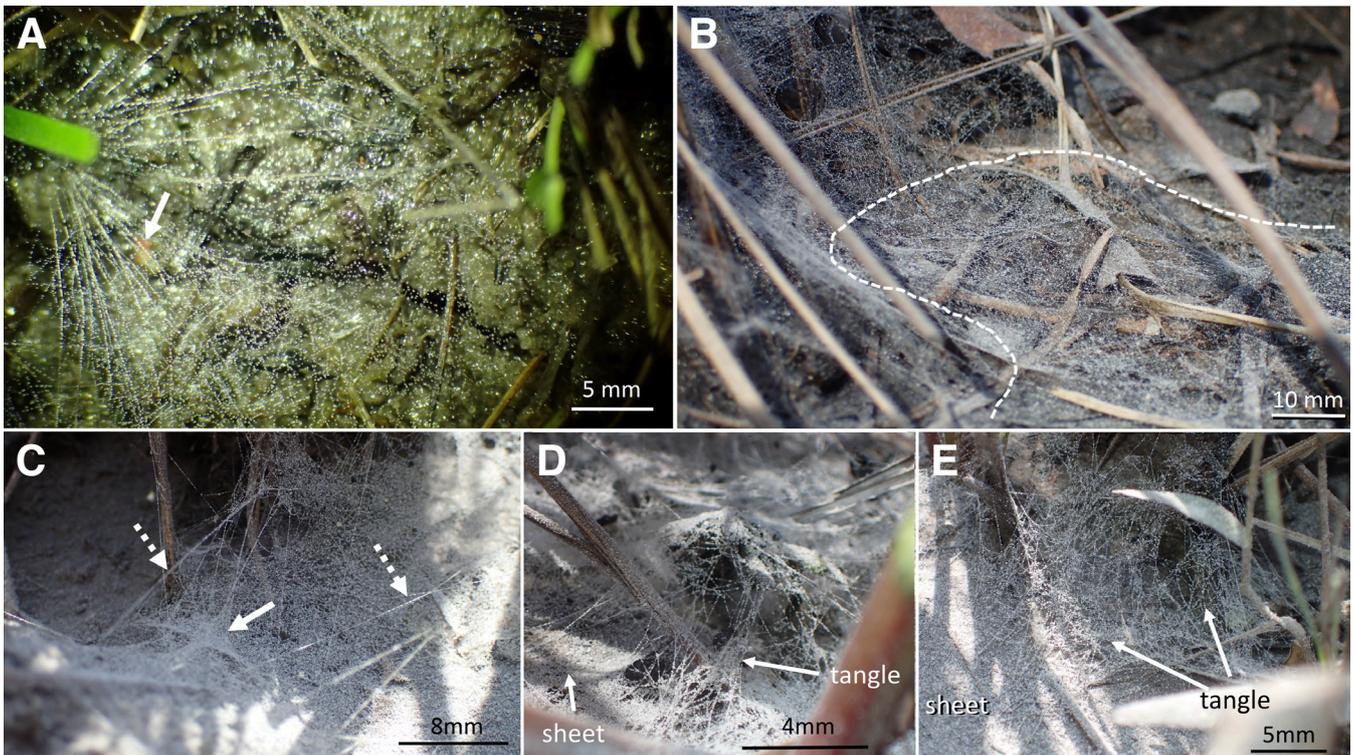


Fig. 4: **A** photo (from directly above) taken the morning after the spider apparently built numerous lines above the body of a large prey (arrow) that it attacked on the sheet and then lowered onto the ground surface below (see text). Multiple lines radiated from a grass blade to the sheet. Similar patterns of multiple radiating lines were not seen in the field; **B** web, seen from above and the side, photographed at about 5 pm in the field; the dotted line traces the approximate border of the portion of the sheet that had sagged into contact with the substrate below; **C** small sub-sheet (solid arrow) near the edge of this sheet, which also had sparse tangle lines above it (photographed from above; some tangle lines are indicated with dotted arrows); **D** multiple upward-slanting tangle lines were attached to an object that protruded upward near the edge of the sheet (seen from above and the side); **E** this web had an extensive tangle of lines (arrows) at one edge of the sheet (seen from above and slightly from the side). The web in **A** is unpowdered and was built in captivity; the others are powdered and were built in the field.

The possible benefit derived from water drops in prey capture poses the question of whether hahniids choose web sites near the surface of damp soil in order to obtain droplets to improve prey retention. Other non-exclusive hypotheses that could also explain the choice of web sites near the soil include greater numbers of prey near the soil (the web design seems most appropriate for prey falling from above), and avoidance of wind damage. Webs very near the surface of damp ground will inevitably accumulate water droplets, and it is possible that the droplets have disadvantages: they may sometimes cause the web to sag into contact with the ground below (Fig. 4B); they may facilitate prey escape by sagging close enough to the ground below that prey can gain purchase on the ground and pull free; they increase web visibility and could facilitate avoidance by prey (Craig & Freeman 1991); and they may make it difficult for the spider to re-ingest lines (if they ever do so) (Eberhard in press). Much remains to be learned about web site choices by hahniids.

Spiders moving across their webs did not accumulate drops of water on their bodies, even though they clearly touched droplets repeatedly. Presumably the mechanism with which *N. riparia* avoided wetting involved the setae that cover their bodies, as in other spiders (Suter, Stratton & Miller 2004).

The absolute durations of prey retention reported here may not be especially important biologically, because *N. riparia* prey on many other species, and I biased the sites where I introduced the ants toward central portions of the web. The observations do demonstrate, however, that prey

can escape using several qualitatively different techniques. Two types of escape, by grasping an object such as a grass stem that projects through the sheet, and by contacting the substrate below, may have important implications for how natural selection acts on web designs and web site choices. Objects projecting through the sheet were common in the field, and in addition to facilitating escapes, they probably also partially obstruct attacks by spiders (Eberhard & Hazzi 2017). Building sheet webs very near the ground has the disadvantage of increasing the chances that prey can grasp objects below and pull themselves free when the sheet sags.

The sheet webs of some other spiders, such as some linyphiids and theridiids, apparently seldom or never have such objects projecting through them (Eberhard, Agnarsson & Levi 2008; Hormiga & Eberhard in prep.). Presumably spiders in these other groups explore sites prior to building, and avoid building where there is insufficient open space. The cluttered nature of the space just above the soil surface may make it difficult for *N. riparia* to find spaces in which to build webs that do not have objects protruding through them.

The consistent rejection of worker *S. invicta* ants by *N. riparia* did not fit Bristowe's claim (1939) (which was not accompanied by quantitative data) that the hahniid *Hahnia helveola* preyed especially on ants. Further observations of other non-exotic ant species that are smaller relative to the spiders are needed to evaluate this contradiction.

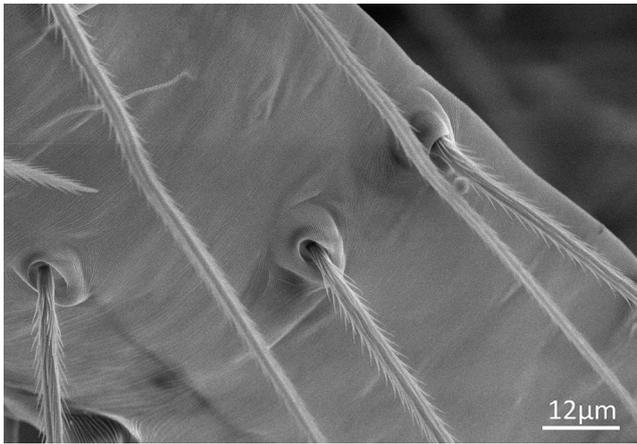


Fig. 5: The surface of the tarsus of the shed cuticle of an immature individual is smooth and lacks obvious irregularities in this SEM image that could confer hydrophobic properties.

### Acknowledgements

I thank Kyle Harms for showing me the study site and useful conversations, Tom Lydon of the Nature Conservancy for permission to work on the Preserve, Paula Calderon for help with the SEM, two anonymous reviewers for useful comments, and (especially) Brent Opell for identifying the spider.

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