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WEBS OF *MIAGRAMMOPES* (ARANEAE: ULOBORIDAE) IN THE NEOTROPICS

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INTRODUCTION

Uloborid spiders (*Uloborus* sens. lat.) typically construct orb webs composed of non-sticky threads (radii, frame threads, hub, and temporary spiral) which support a sticky spiral made of cribellar or hackled silk. Specialization of the web in the uloborid genus *Miagrammopes* has involved the reduction of its structural complexity together with changes in its operation as an insect trap. The one described web of an unidentified species from Natal, South Africa is reduced to a single horizontal capture thread (Akerman 1932). In this paper we describe the webs of six more species of *Miagrammopes* and the prey capture behavior of the spiders, revealing a substantial range of variation in simple web design within the genus.

We studied *M. simus* on Barro Colorado Island, Panama Canal Zone during the wet season of 1976. At no time was this species common. In May and June, 1977, *M,* sp. 1 (ca. *unipus*) was studied in a bamboo (*Guadua angustifolia*) thicket in the Cauca valley near Cali, Colombia where it occurred in abundance. In August, 1977, *M. intempus* Chickering and *M.* sp. 2 were found in Valle, Colombia. The former was common in some places on hanging moss on exposed roots and low branches near the Rio Anchicayá at 400 m elevation, while the latter was found in brush near the Rio Tuluá at 1100 m elevation. A small tree in a clearing on Finca La Selva

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near Puerto Viejo, Heredia Province, Costa Rica, had substantial populations of *M.* sp 3. *M.* sp. 4 was found on low vegetation in January and February, 1978, in mid-elevation wet forest in Guatopo National Park, Miranda State, Venezuela. Individuals of the last four species were observed in the field on only one or two days each, but in all cases more extensive observations had already been made on the other species, and it was thus possible to make critical observations allowing comparisons among all six species. *Miagrammopes* sp. 1–4 appear to be either undescribed species or females of species known only from males. Voucher specimens of these and of the two previously described species are deposited in the Museum of Comparative Zoology, Harvard University.

The Webs

M. simus

The web typically consisted of a single vertical capture thread about 1 m long, attached above to a short, horizontal resting thread strung under a leaf, and below to the ground or a leaf or twig (Fig. 1a). The capture thread was covered with sticky, cribellar silk along the central 50 to 60 percent of its length, and one or more very fine, more or less horizontal threads often connected it to other supports. Both end portions of the capture thread were non-sticky. For an individual whose webs were measured periodically, the lengths of sticky and non-sticky sections in new webs were (in cm; lengths of sticky portions underlined): 20:$\underline{50}$:30, 4:$\underline{50}$:30, 6:$\underline{52}$:34, 7:$\underline{60}$:32, and 7:$\underline{60}$:34. One adult female which had been starved for seven days made a web with two vertical capture threads and several thin, non sticky lines between them.

One *M. simus* was seen laying sticky, cribellar silk on a non-sticky, vertical thread which was already in place. The spider moved slowly up the thread, combing out silk with legs IV until it was about 5 cm below the resting thread, then ran up and assumed the resting posture.

Individuals of *M. simus* rested under the horizontal thread and held onto the broken end of the capture thread with one leg I and one leg II, while the other legs held the resting thread (Fig. 1b). Tension was exerted on the vertical capture thread both by pulling it up with leg I and by backing up and pulling in the resting thread with the fourth pair of legs. The spider which constructed a web with two

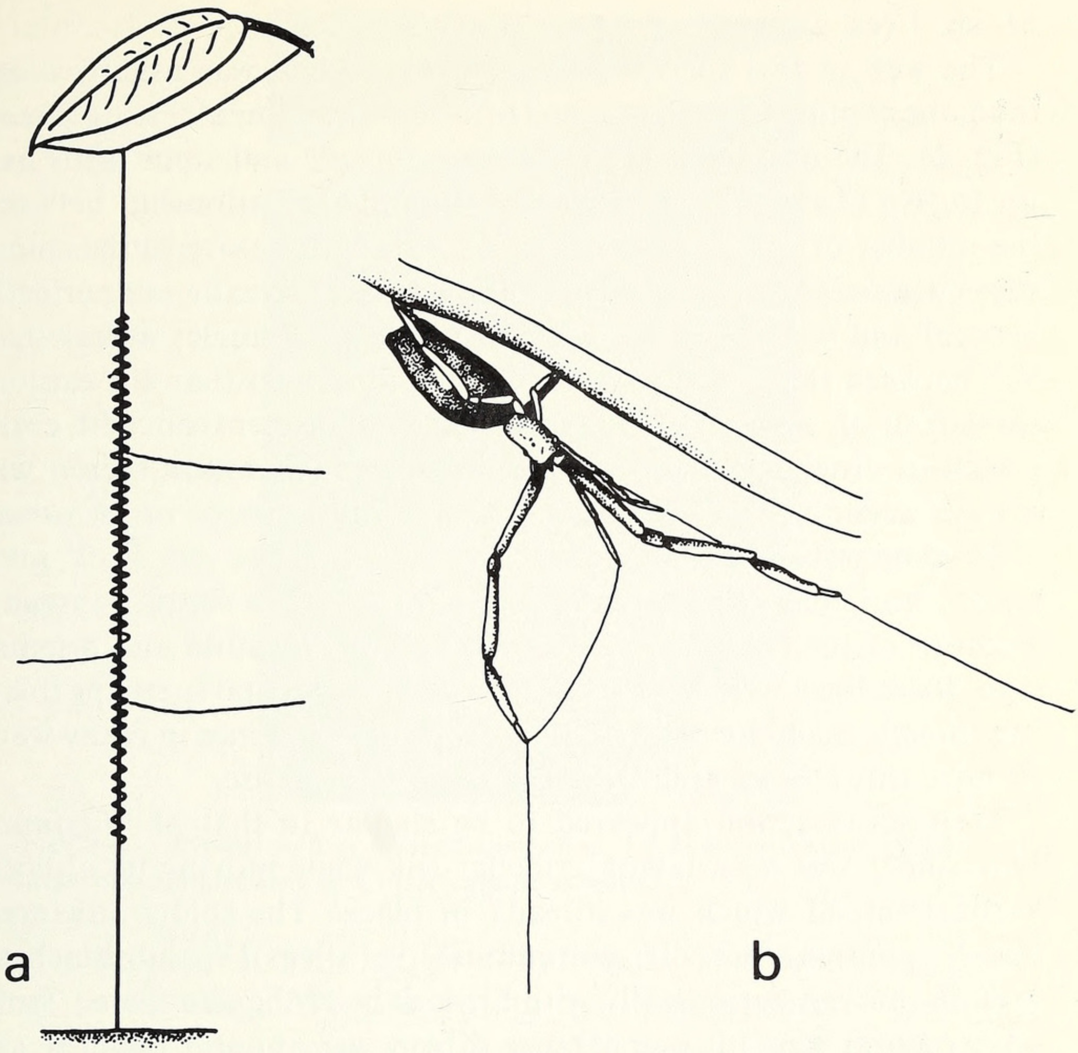

Figure 1. a) Typical web of *Miagrammopes simus,* showing the horizontal resting thread under a leaf, the vertical capture thread with sticky segment and thin, non-sticky, horizontal threads; b) posture of *M. simus* as it holds its web and waits for prey.

capture threads rested in essentially the same position; the leg I holding the horizontal resting thread was in position to monitor vibrations from the second capture thread.

When disturbed, or when hanging from a resting thread with no capture thread present, *M. simus* assumed a stick-like, cryptic posture, orienting along the resting thread with the first and second pair of legs held straight forward and the fourth pair held straight behind. The small third pair of legs held the resting thread or the substrate, but were pressed close to the body and did not break the stick-like outline.

M. sp. 1 (ca. *unipus*)

The web of this species differed in that there was usually more than one capture thread attached to a single horizontal resting thread (Fig. 2). The average was 2.4 capture threads and some webs had up to five (Table 1). There was no apparent relationship between the number of capture threads in the web and the size of the spider that constructed it. The capture threads were usually not perfectly vertical and were often in different planes with angles of less than 90° between them. They were shorter and thinner than the capture threads of *M. simus* and it was necessary to powder them with corn-starch in order to count them. The horizontal resting thread was always under a thin twig rather than a leaf, as in webs of *M. simus.*

In some webs of *M.* sp. 1 there were one or more very slack, non-sticky, horizontal threads connecting the multiple capture threads. Because of their looseness and their variable location and orientation, these lines were at first thought to be incidental (perhaps floating threads made by other spiders), but their presence in many webs of both this species and *M. simus* argues otherwise.

Web construction appeared to be similar to that of *M. simus.* One spider was seen laying cribellar silk while moving up along a vertical thread which was already in place. The spider advanced slowly, combing out silk continuously with legs IV and attaching it to the thread periodically with brisk dabs of the abdomen. Total construction time for one capture thread was about 3 minutes.

At night, *M.* sp. 1 assumed a capture position similar to that of *M. simus,* resting under the horizontal thread and holding a capture thread with legs I and II (Fig. 1b). During the day it either held the capture thread in the same way, or, more often, assumed a more cryptic resting posture. The spider positioned itself near one end of the resting thread which it broke and spanned with its body. It held one end with one or both pairs of front legs, and then pulled in the line behind it with the hind legs (and, occasionally, the

Table 1. Numbers of sticky capture threads in 66 webs of *Miagrammopes* sp. 1 (ca. *unipus*) and 22 webs of *M.* sp. 3.

	Number of Capture Threads					
Number of Webs	1	2	3	4	5	6 or more
M. sp. 1	15	21	22	6	2	0
M. sp. 3	4	5	3	3	6	1

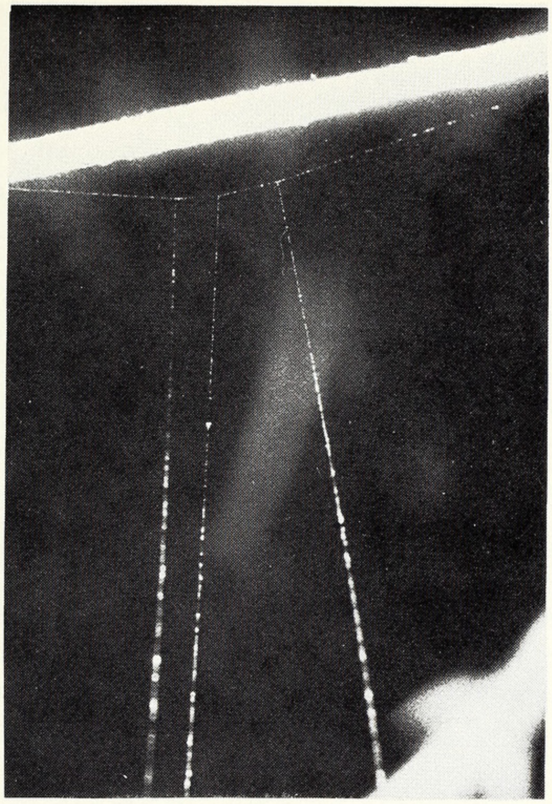

Figure 2. Typical web of *Miagrammopes* sp. 1 (ca. *unipus*) showing horizontal resting thread under twig and three capture threads.

line in front of it with legs I). The result was to draw the spider close to the twig. When adopting the cryptic posture, the spider reached out briefly with legs II and III to pull itself closer to the twig, then positioned legs II against legs I, holding the broken end of the resting thread, and legs III against the sides of the abdomen. In this position it was nearly invisible (see Fig. 3).

M. sp. 2

The web of one adult female was found in the morning (the spider was without a web at 2100 the night before), and was similar to some of the webs of *M.* sp. 1. The spider rested pressed to the undersurface of a branch, at the end of a horizontal thread about 3 cm long that was strung under the branch (Fig. 3). She held the broken end of the horizontal thread with one leg II and kept it tense by pulling in the thread with her hind legs, as described for *M. simus* and *M.* sp. 1. A single, vertical, capture thread (invisible until powdered) was attached near the other end of the horizontal thread. The lengths of the non-sticky and sticky portions of the capture thread were 7:53:40.

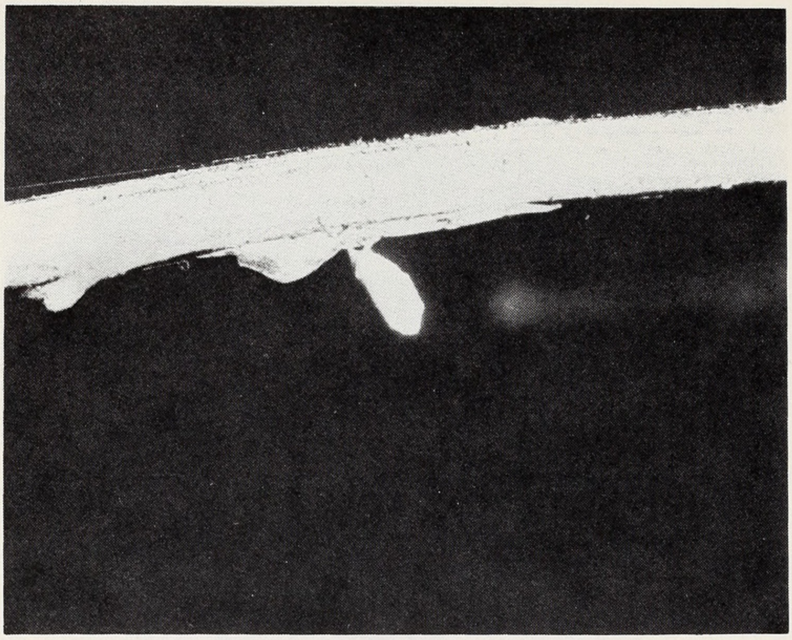

Figure 3. *Miagrammopes* sp. 2 in cryptic posture as it feeds and holds the non-sticky resting thread.

M. intempus

Webs of this species were variable and most were different from those of other *Miagrammopes* species. One mature female held both a horizontal and a vertical sticky thread with her front legs, and a single, short, non-sticky line with her rear legs (Fig. 4). A second female also held two capture threads, but both were at an angle rather than being either horizontal or vertical. The first spider was induced to move forward along the horizontal thread several times and her return to the waiting position was observed carefully (Fig. 4). Each time she tensed the sticky threads by pulling them in with her front legs; she did not move her hind legs. Another individual, on a web which was similar except that the horizontal thread did not appear to be sticky, held the sticky vertical thread in the same way that *M. simus* held the capture thread and tensed it by pulling thread with both front and hind legs. Still other individuals with single, horizontal, sticky threads (Fig. 5) failed to pull in silk as they assumed the waiting position. One vertical thread had several very fine, loose, horizontal lines attached to it, similar to those shown in Fig. 1a for *M. simus*.

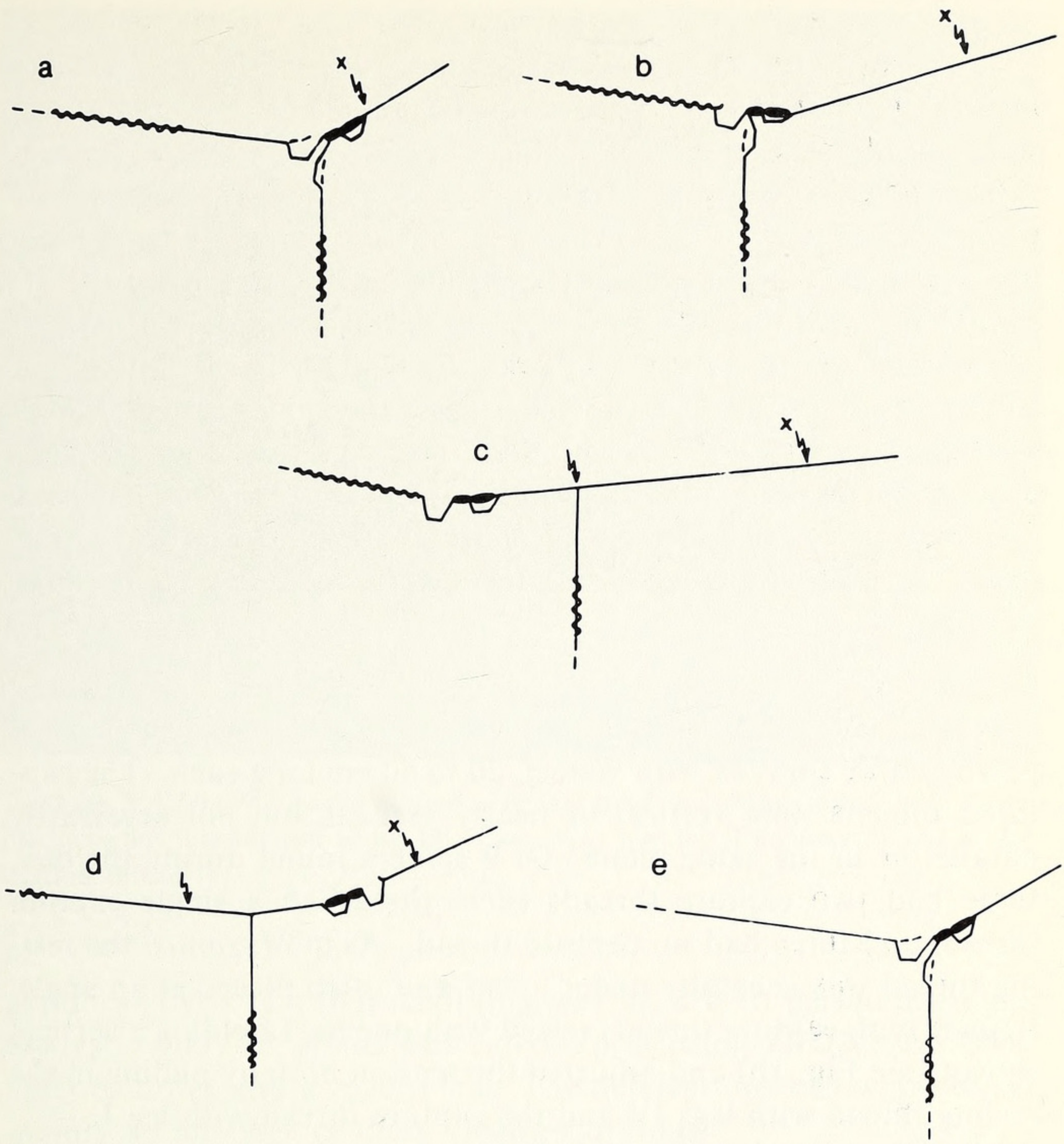

Figure 4. Movements of a female *M. intempus,* illustrating how thread attachments are manipulated. Letters mark spots on horizontal thread. The spider rested (a) holding both sticky lines with its front legs, and a third, short, non-sticky line with its hind legs at point *x* (the ends of the capture threads were not drawn as they could not be seen). When lured out onto the horizontal sticky line, the spider carried the vertical thread for some distance (b), then attached it to the horizontal line and continued on (c). When she returned, she shifted the point of attachment of the vertical thread again (d), then turned around and pulled in the line with her front legs and resumed her original position (e). The shifts in attachment were extremely rapid; the actual motions involved could not be followed, and the shifts were noticed only by comparing thread positions before and after the spider passed by.

M. sp. 3

The webs of this species were similar to those of *M.* sp. 1 in having variable numbers of capture threads (Table 1). The sticky lines were not all attached to a non-sticky line at one end, however, but rather radiated in several directions from a more or less centrally placed thread (Fig. 6). The spider rested on this thread, often breaking one of the capture threads and holding it as described for *M. simus* (Figs. 1b and 6). This position was also similar to that of *M. intempus* in that the spider held a non-sticky line behind it and a sticky line in front of it. In other cases the spider rested holding only the non-sticky thread with both front legs. The sticky threads differed from those of other species of *Miagrammopes* in being relatively short (all less than 25 cm) and sticky all the way to the lower end. The webs were found at night and were gone the next morning.

M. sp. 4

Webs of *M.* sp. 4 had one or two capture threads (invisible until powdered or sprayed with water), 20 to 40 cm long each. The captured threads were vertical or nearly vertical, but not necessarily parallel or in the same plane. Of 9 spiders found during the day, three had two capture threads each, three had a single capture thread, and three had no capture thread. As in *M. simus,* the resting thread was generally under a leaf and often placed at an angle. Spiders with capture threads rested with one leg I holding a vertical thread (see Fig. 1b) and adjusted the tension both by pulling in the resting thread with legs IV and the capture thread with leg I.

Spiders without capture threads rested in a cryptic position similar to that of *M. simus.* Often after going into the cryptic posture (and particularly when disturbed), the spider bounced up and down on the resting thread in a rhythmic motion reminiscent of rocking motions of stick insects (Phasmidae). The significance of these movements is not known.

Prey Capture

We observed in detail prey captures made by four *M. simus,* two *M.* sp. 1, and one *M. intempus.* Insects that we gave to the spiders as prey included fruitflies (2–3 mm long), moths (3–7 mm long), and ants (3–5 mm long). In general, the sequences of prey capture behavior were similar, but the spiders moved so rapidly that stop-

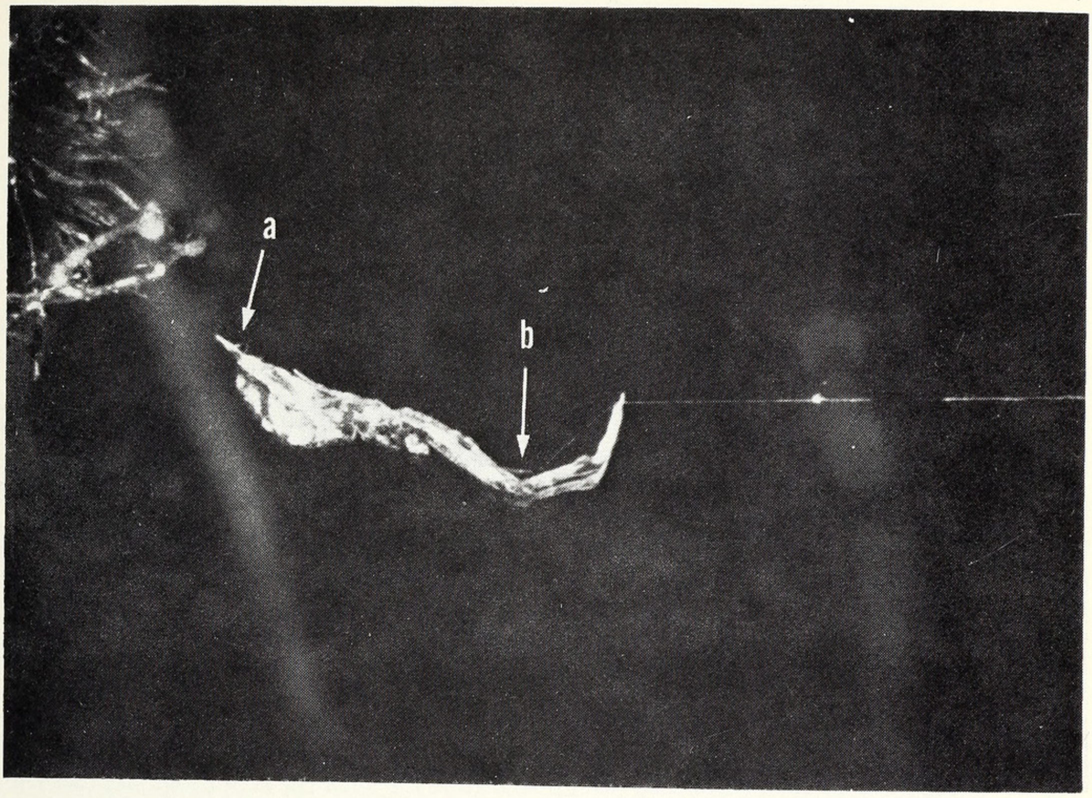

Figure 5. *Miagrammopes intempus* female holding a single thread web. Note the loose line just anterior to the tip of leg IV(a), and leg II holding the end of the capture thread (b).

action analysis of video-recording was needed to permit adequate analysis. Only *M. simus* was video-taped, using a SONY AV-3400 videorecorder and a macro lens. The descriptions below are based mainly on analyses of these video-recordings.

Stage I: Prey detection — jerking the capture thread

When an insect was placed on the capture thread, the spider responded by jerking the thread, The spider quickly flexed her lower leg I, which held the capture thread, and immediately extended it again. The maximum distance travelled by the tip of the leg on an upward jerk was 0.3 leg length (about 2.8 mm), and the quickest jerks were accomplished in less than 1/60 second (the time span of a single "frame" of the video-recording). It is tempting to think that jerking functions in gauging the weight or size of the prey, as seems to be the case in other uloborids (Eberhard 1969). Spiders with multiple capture threads (both *M.* sp. 1 and *M. simus*) jerked only the thread on which prey had been placed.

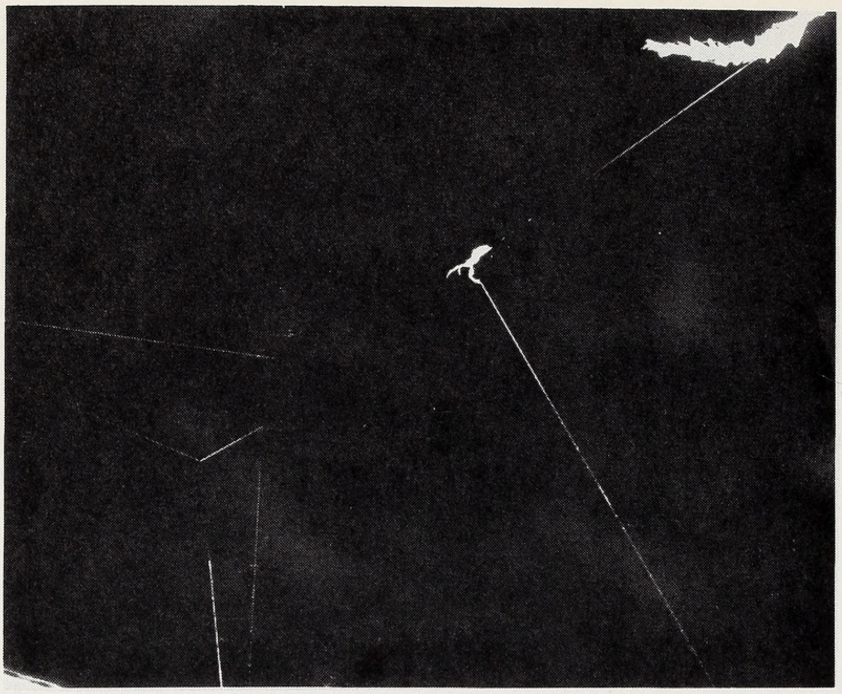

Figure 6. *Miagrammopes* sp. 3 on its web, as seen from below and slightly to the side. The brighter threads are sticky (the web was not powdered). Note that the spider has broken the end of the capture thread and holds it with the front legs bent to the side in a manner similar to that shown for *M. simus* (Fig. 1 b).

Stage II: Entanglement of the prey — sagging the line

The spider sagged the capture thread by dropping the loose silk it had pulled in with its hind legs, and perhaps also letting out additional dragline. At almost the same time it manipulated the capture thread with a series of complex movements of leg I (Fig. 7a) which resulted in the prey being jerked rapidly back up and down again (Fig. 7b). Whereas the jerks in stage I displaced a fruitfly only 5–6 mm, sagging the capture thread caused the prey to drop 26–33 mm in less than 1/30 second. As the prey dropped, it was often displaced sideways as much as 6 mm (due to air currents?). Rapid and repeated sagging of the capture thread resulted in the formation of one or more loops of silk that enveloped the prey. Such loops were seen in the capture threads of both *M. simus* and *M.* sp. 1.

The mechanism responsible for the formation of these loops is not clear. One possible explanation is that, due to the relatively higher air resistance and lower weight of the silk, the prey drops more rapidly than the silk during a sag, and therefore falls into the silk below it (Fig. 8a). An alternative explanation (Fig. 8b) is that, at the end of a sag, when the spider jerks the line up again, the prey is "snapped" back upward and accelerated more than the silk just above it so that it "runs into" the thread above it. The second of these hypotheses is more appealing since 1) it would work with non-vertical capture threads whereas the first would not, and 2) we saw two instances in which a loop clearly formed in the thread just above the prey. In any event, the spider is somehow able to entangle the prey from a distance by manipulating the capture thread.

Stage III: Immobilization of prey-wrapping

After manipulating the capture thread to cause one or more sags,

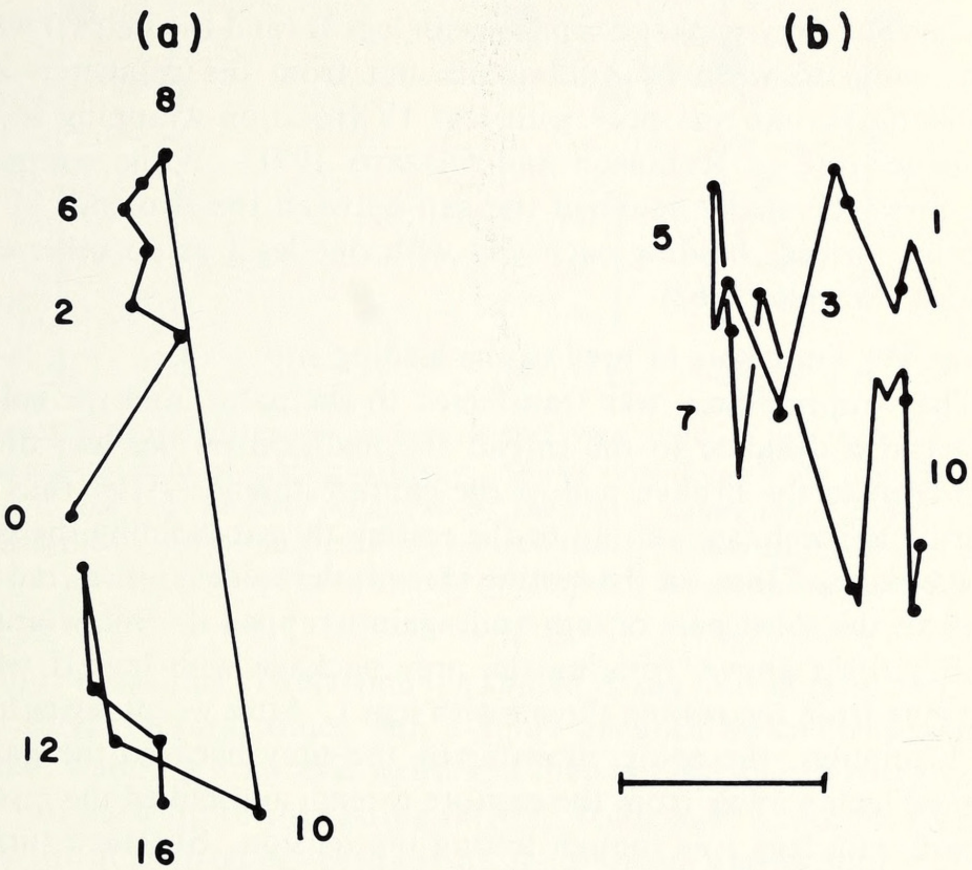

Figure 7. a) Movements of the tip of leg I of a female *Miagrammopes simus* as she sagged the capture thread. Points are locations of the tip of leg I holding the capture thread, taken from a video-taped sequence with "frames" 1/60 sec apart. In frames 3–5 the tip of the leg remained in the same spot. In frames 9 and 11 the tip of the leg was not visible; these points are not shown in the figure. b) Movements of a prey on the capture thread while the thread is being sagged and jerked back up and down, taken from a video-taped sequence (as above). Numbers refer to segments of the path of movement of the prey on the line during consecutive 1/60 sec intervals. Scale marker represents 10 mm.

the spider attached a dragline to the resting thread and moved rapidly down the capture thread, pulling in the capture thread and wadding it up loosely with legs II as it moved. It touched the prey one or more times with legs I, probably receiving tactile and chemical clues as to the identity of the prey, and then turned 180° and began wrapping. The wadded up capture thread was transferred to legs III and wrapped onto the prey, probably thereby increasing the effectiveness of the initial wraps.

While wrapping, the spider faced away from the prey, holding the capture thread just above the prey with one leg I and the prey itself with legs II and III. After 20–30 seconds of wrapping, the spider cut the capture thread just above and below the prey. It then rotated the prey package rapidly with legs II (and the palps?) while continuing to wrap by pulling silk out from the spinnerets and throwing it onto the prey with legs IV (rotation-wrapping in the nomenclature of Robinson and Olazarri 1971). While wrapping the prey, the spider spanned the gap between the two ends of the capture thread, holding each end with one leg I as do other uloborids (Marples 1962).

Stage IV: Transport of prey to the feeding site

The wrapped prey was transferred to the palps, and the spider attached a dragline to the thread she had laid on her way down and then to the broken end of the capture thread. After thus repairing the web, she ran up to the resting thread, holding the prey in the palps. Once on the resting thread, the spider transferred the prey to the third pair of legs and again wrapped it. She wrapped as described above, rotating the prey package with legs II while hanging from the resting thread with legs I. After wrapping as long as 5 minutes, the spider transferred the prey back to the palps, turned facing away from the capture thread, and pulled the resting thread with legs I as though testing the tension. She then turned 180° and resumed a resting posture with one leg I monitoring the capture thread. As in other uloborids, the prey package was held "overhead" in the palps and chelicerae while the spider fed (Fig 3) and re-wrapped several times during the process of feeding. Feeding often lasted an hour or more.

Variations in the prey capture sequence

We saw several modifications of the basic prey capture sequence in *M. simus*. Small dolichoderine ants were rejected by a spider

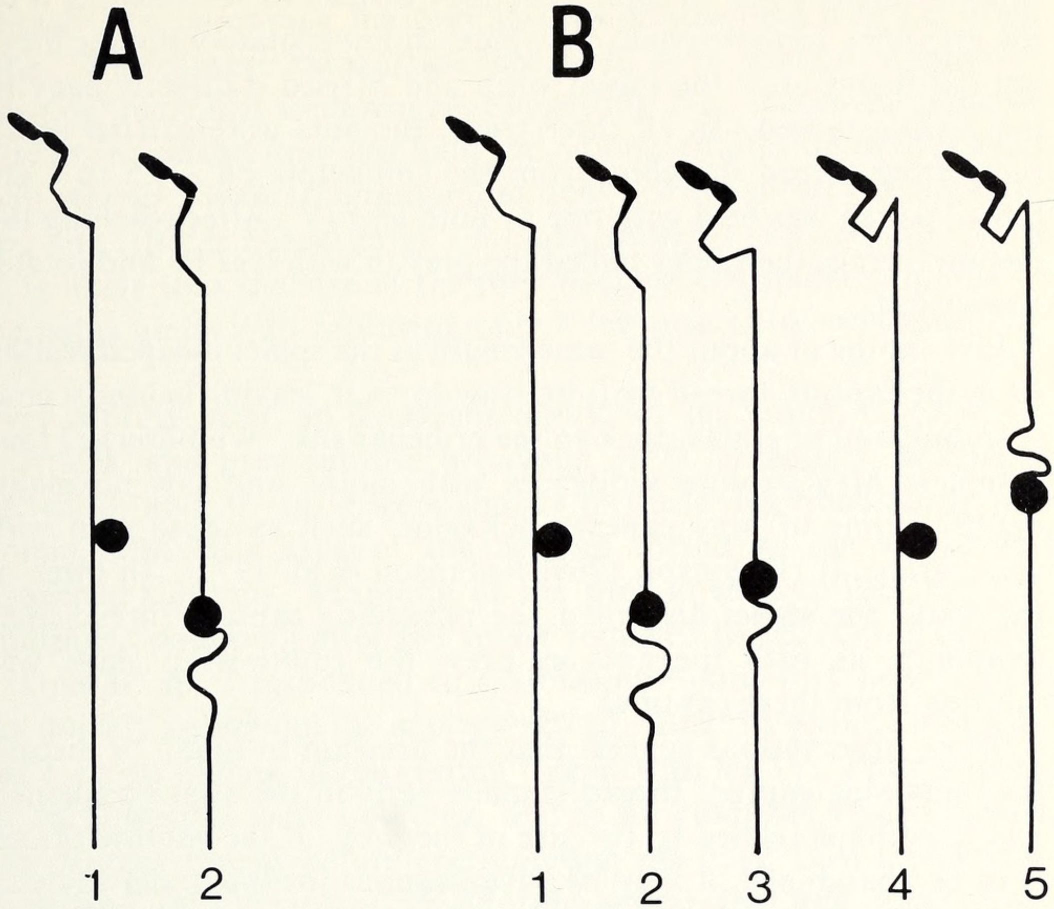

Figure 8. Two possible mechanisms which could result in prey becoming entangled as a result of sagging behavior. A) The prey drops faster than the line below it, and thus becomes entangled. B) The prey's momentum, acquired when the spider jerks the line up after a sag, causes it to become entangled in the line just above it. This hypothesis depends on the thread below the prey being extensible.

on four occasions. Each time the spider jerked and sagged the capture thread several times, ran a short distance down the capture thread, wadding it up as it went, and then cut the line above the ant and ran back up to the resting thread. These ants were thus recognized from a distance, perhaps by their strong alarm odor. After an ant was rejected, the wadded-up section of the capture thread was manipulated in the mouthparts for several minutes (feeding?), then dropped. Rejection of prey thus resulted in destruction of the capture thread. A new thread was often built within a few hours.

Three other ants, two *Camponotus* sp. and one *Ectatoma* sp., all about the same size as the spider (6–7 mm long), were attacked successfully, but modifications of the capture sequence occurred in all three trials. In two, the spider dropped the lower portion of the capture thread after wrapping the prey instead of re-attaching it to the dragline. In these trials, the spider did not rotate-wrap the prey, but cut it out after the initial wrap and carried it directly back to the resting thread. In all three trials, the ants were carried up to the resting thread dangling from the spinnerets on a 1.5 to 2 cm thread which was held with one or both legs IV. After reaching the resting thread, the spider pulled the prey in with legs IV and rotate-wrapped it.

Live moths of about the same length as the spider escaped readily from the capture thread by fluttering down it, leaving behind a conspicuous trail of scales stuck to the cribellar silk. We observed four complete prey capture sequences with moths and saw no major modifications in prey capture behavior, such as those seen with some araneids (Robinson 1969, Robinson et al. 1971). In three of the trials, the spider discarded the remaining capture thread after wrapping; as with the ants as prey, the rotate-wrap stage was omitted from these captures.

These observations suggest that the decision to retain or discard the remaining capture thread is made early in the attack sequence, and is perhaps related to the size of the prey. If the capture thread is to be abandoned, it may be advantageous for the spider to delay rotation-wrapping until it reaches the resting thread, where it is less exposed to visual predators. This explanation is not entirely satisfactory, however, since if rotation-wrapping is not necessary at the capture site (it would seem most necessary for just those large prey for which it is omitted), it would seem advantageous to perform all rotation-wrapping at the more protected resting thread.

Capture sequences with multiple prey

Capture of small prey such as fruitflies caused little damage to the capture thread, because the repair of the thread left the remaining sticky portion intact. When presented with a second or third prey, the spider rushed down the capture thread holding the first prey in its palps, and attacked the new prey in the usual manner. Second prey were wrapped together with the first prey and carried up to the resting thread in the palps in one large package, or wrapped separately and carried up hanging from the spinnerets, then wrapped with the first prey.

After only a few prey items were captured, the spider destroyed the remaining capture thread by dropping the lower end of the thread after wrapping the prey instead of attaching it to the dragline. The capture thread was destroyed even when a substantial portion remained undamaged, suggesting that the catching capacity of the thread does not limit the number of prey items the spider will attack. Since *Miagrammopes* does not attach prey at the feeding site (this is also true of *Uloborus diversus* — Eberhard 1967), it is likely that the size of the prey package the spider can hold in its palps limits it to capturing only a few insects in succession.

Prey capture in *M.* sp. 2, *M. intempus, M.* sp. 3, and *M.* sp. 4

Attack and prey capture behaviors of *M. intempus, M.* sp. 2, *M.* sp. 3, and *M.* sp. 4 were similar to those described above, involving dramatic sags of the capture thread as the spider approached the prey, wrapping of the prey at the capture site, and continued wrapping after the spider returned to the resting thread.

One *M.* sp. 3 responded to a vibrating tuning fork held nearby by quickly tightening the capture thread, either by pulling it in with leg I or by pulling in the resting thread with leg IV. Four attacks of *M. intempus* were observed, and in all cases the spider sagged the capture thread before encountering the prey, then attacked it by wrapping. One insect, an odorous pentatomid bug, was tapped repeatedly with the front legs before being wrapped and discarded. In one sequence it was possible to ascertain that the sticky capture thread was wadded up as the spider approached the prey, and was laid onto it as wrapping began.

Prey species captured

Prey taken from webs of an unidentified *Miagrammopes* sp. in Bayano, Panama which constructed a web with a single capture thread like that of *M. simus* included the following insects: 1 wasp, 1 winged ant, 2 nematocerous flies (1 psychodid), and 1 unidentified. An additional 29 prey collected as *M.* sp 1 fed on them included 14 winged ants of two species, 3 wasps, 2 nematocerous flies, 2 other flies, 1 beetle, and 7 unidentified insects. Four flies were collected as *M.* sp. 3 fed on them: 2 nematocerans of probably different families, a dolichopodid fly, and one acalyptrate. One small beetle was taken from an immature *M.* sp. 4. These lists make it clear that the spiders prey on a wide variety of insects, and are not specialists on any one group.

Reproduction

The egg sac and its web

The egg sacs of *M. simus, M.* sp. 1, *M.* sp. 3, and *M. intempus* were tubular and elongate, two to four times the length of the spider, and very similar in color to the adult female. The egg sacs of *M. simus* and *M.* sp. 1 were brown, while those of *M.* sp. 3 and *M. intempus* were lightly coated with green silk. The sacs were thin-walled, with no fluffy silk inside, and the outlines of the eggs, which were arranged in one or two rows, were clearly visible.

The females stayed by the egg sacs during the day, either in a stick posture in line with the sac (Fig. 9) or holding one end of it with leg I, as seen in some *M.* sp. 1. In these positions both the spider and the egg sac were difficult to recognize; they looked like a dead twig. One *M. simus* female remained with an egg sac containing 52 eggs for 2 weeks in an outdoor cage. During this time she did not construct a capture thread. One *M.* sp. 1, however, nightly abandoned the daytime cryptic posture and laid several more or less horizontal, radial lines, suspending the sac by one end from the "hub" of this tiny web (Fig. 10). A single jagged loop of sticky silk was laid and the spider rested under the hub. When a

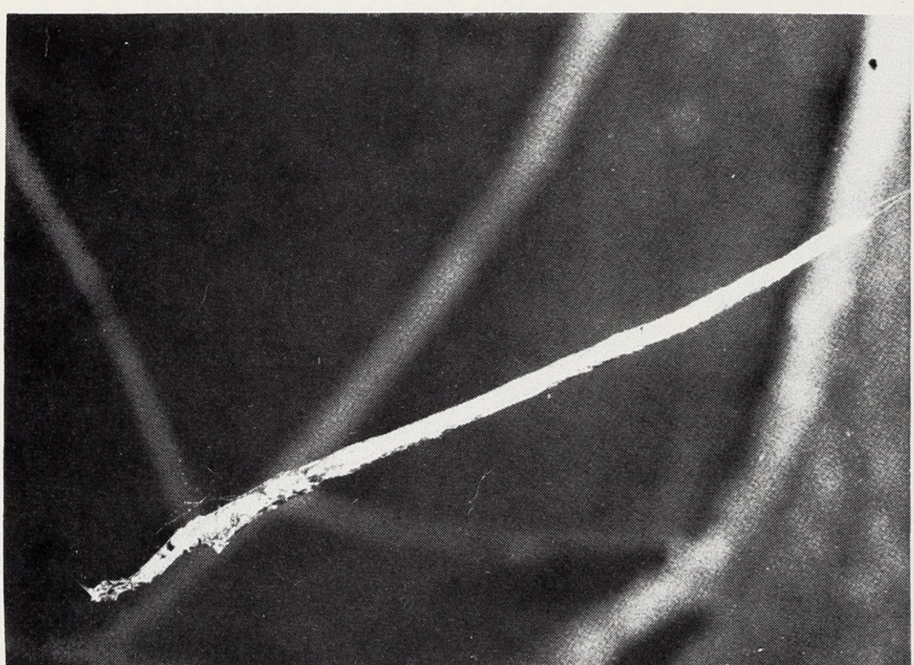

Figure 9. Daytime posture of a *Miagrammopes* sp. 1 (ca. *unipus*) female with an egg sac.

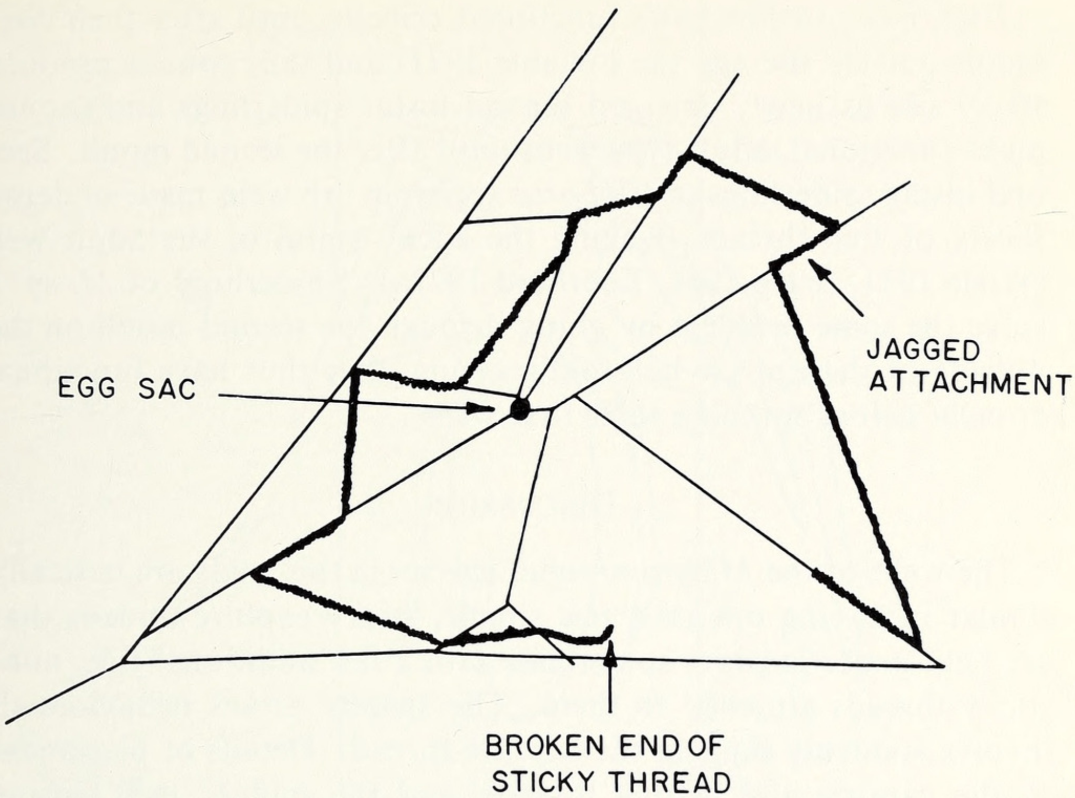

Figure 10. Egg sac web spun at night by a *Miagrammopes* sp. 1 (ca. *unipus*) female. The horizontal web is seen from above, with the tubular egg sac hanging down from the "hub." One end of the sticky "spiral" hung free and had probably been connected to the radius just to its right. The spider rested near the hub, out of contact with the egg sac.

small insect was placed on the sticky silk, the spider attacked and fed on it. During the day this rudimentary orb was gone, and the spider was back in the cryptic posture at the end of the egg sac.

Emergence of spiderlings

We observed emergence of spiderlings from one egg sac of *M.* sp. 1. The spiderlings were first seen one evening easing themselves through several ragged holes in the sac. They left behind, inside the empty sac, empty egg shells each with a pink moulted skin stuck to it. These second instar spiderlings (terminology of Hite, et al. 1966) were relatively inactive and stayed on the sac itself, holding their anterior legs in an unusual position (Fig. 11). The next morning, they had all moulted again, and the cast skins remained on the surface of the egg sac while the spiderlings wandered actively in the vial, holding their legs normally. These spiderlings (third instar) had fully developed cribella and calamistra.

Uloborids do not have functional cribella until after their first moult outside the egg sac (Wiehle 1931) and thus cannot produce sticky silk as newly emerged second instar spiderlings and cannot make functional, adult-type webs until after the second moult. Second instar spiderlings of *Uloborus* spp. spin orb webs made of dense sheets of fine threads, lacking the sticky spiral of the adult web (Wiele 1931, Szlep 1961, Eberhard 1977a). Spiderlings of *M.* sp. 1 solve the same problem by going through the second moult on the outside of the egg sac before dispersing; they thus have functional cribella before spinning their first webs.

Discussion

The webs of the *Miagrammopes* species in this study are basically similar in having one or a few simple, sticky capture threads that are held under tension, sometimes with a few additional fine, non-sticky threads attached to them. The spiders' attack behaviors all involve suddenly sagging the capture thread. Details of placement of the capture and resting threads, and the spiders' web tensing behavior are variable among the species, and even to some extent among individuals of some species. Two of the characteristics described for *M.* sp. 1 appear to be unique among spiders — the double moult of the young before leaving the egg sac, and the special feeding web of the female near her egg sac.

The web of *Miagrammopes* species from Natal was similar to some of the webs of *M. intempus* and *M.* sp. 3 in having a single horizontal capture thread without a separate resting thread (Akerman 1932). The presence of additional fine threads attached to the capture thread was not noted in webs from Natal, but they would almost surely have gone unnoticed unless the webs were powdered. Web construction behavior was similar in the Natal species. The spider sat at one end of the completed capture thread, facing it; the thread may have been broken with the spider bridging the gap with its body (e.g. Marples 1962), but Akerman's drawing shows an intact line. The thread was held under tension by pulling it in with legs IV as do all six species of this study and was also quickly sagged when prey hit it. The single, horizontal, capture thread web may represent a further simplification of an already simple web, with a single sticky thread taking the place of both the horizontal resting thread and the vertical capture thread.

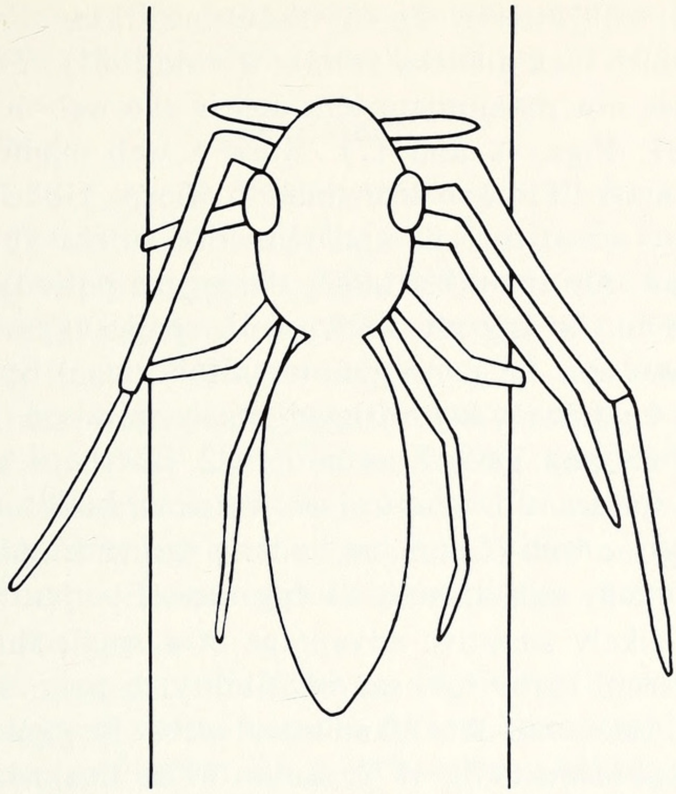

Figure 11. Typical leg positions of second instar *Miagrammopes* sp. 1 (ca. *unipus*) as they rested on the outside of the egg sac.

Although uloborids in general seem to construct their webs in the early morning (e.g. Eberhard 1972, Lubin and Eberhard unpubl.), *Miagrammopes* are more variable. Thus, while *M. simus, M.* sp. 1, and *M.* sp. 4 tend to have webs up early in the morning, they, as well as the species from Natal (Akerman 1932) sometimes build at other times, and *M. intempus* and *M.* sp. 3 commonly build in the evening. An unidentified species in New Guinea which spins single, horizontal threads also tends to build at night (Robinson and Robinson 1974, M. Robinson, pers. comm.). Readiness to build at different times of the day might be expected in view of the rapidity with which new webs can be made and the small investment of material which they represent. The tendency to discard webs support this idea.

Kaston (1964) suggested that the reduced web of *Miagrammopes* is derived from a *Stegodyphus*-type web (Eresidae) which consists of irregularly spaced radii with connecting sticky threads. A web similar to that of *Sybota* (Uloboridae) seems to us a more likely precursor of a *Miagrammopes*-type web. *Sybota producta* (Sim.)

lays cribellar silk directly on the radii and frame threads of orb-like webs which lack a sticky spiral (Wiehle 1931). The spider apparently does not manipulate tensions in the web once it is built (Wiehle 1931: Figs. 14 and 17). Such a web might conceivably become reduced to a web like that of *M.* sp. 1 by loss of frame and auxiliary spiral threads and reduction of the hub to a single resting thread. On the other hand, the jagged pattern of the sticky spiral found in the egg sac webs of *M.* sp. 1 suggests an affinity with *Uloborus* (sens. lat.) or *Hyptiotes* (Uloboridae). Spiders of both these genera commonly lay a jagged, sticky spiral on the periphery of the orb (McCook 1889, Eberhard 1972, Eberhard, unpubl.). An unidentified species of *Uloborus* (*sensu strictu*) builds an essentially identical egg sac web (Eberhard, in prep.), and *Uloborus diversus* also places sticky silk around its egg sacs (Eberhard 1969).

The most likely adaptive advantage of a single thread capture web would seem to be its near invisibility to prey, since at least some flying insects can detect and avoid webs (Bristowe 1941, Robinson and Robinson 1970, 1973, Lubin 1973, Buskirk 1975, Eberhard in prep., Lahman and Zuniga in prep.). This is apparently ruled out, however by the fact that at least two species (*M.*sp.3 and the New Guinea species) and perhaps a third (*M. intempus*) usually build their webs at night when visibility is probably unimportant.

Another possible advantage would be that predators using webs as cues to the presence of prey would be unlikely to detect webs of *Miagrammopes*. Some predators may use webs in this way, though some are known not to (Eberhard 1970). The significance of the very thin, slack lines attached to the capture threads remains even more of a mystery.

The obvious disadvantage of a single thread capture web is the low probability of a flying insect striking the web. Robinson and Robinson (1976) suggested that the numerous nematocerous flies which tend to rest on non-sticky spider threads might try to alight on *Miagrammopes* capture threads and thus become entangled. Indeed Akerman (1932) noted a number of "gnats" caught by the *Miagrammopes* species in Natal. Some nematocerous flies were among the prey collected in this study, but many other kinds of small insects were collected as well. Certainly the webs of *Miagrammopes* are not specialized to the extent of exclusively or even principally capturing nematocerous flies which alight on them. Some other spiders with reduced webs use chemical attractants for specific kinds of prey (Eberhard 1977b), but the wide variety of captured prey rules out this prey capture technique for *Miagrammopes.*

SUMMARY

The webs of six species of *Miagrammopes* (Uloboridae) studied in Panama, Colombia, Costa Rica, and Venezuela have only one or a few sticky capture threads. *Miagrammopes simus* and *M.* sp. 2 have one vertical capture thread attached to a non-sticky, horizontal resting thread. *Miagrammopes* sp. 1 (ca. *unipus*) builds from 1 to 5 near-vertical capture threads, and *M. intempus, M.* sp. 3, and *M.* sp. 4 use one or more capture threads that vary in their spatial arrangement. Webs are pulled taut by pulling in silk with either the front legs or the hind legs or both. The spiders assume highly cryptic postures during the day as they rest on their webs or near the egg sac.

Attack and prey capture behavior in all species involves rapid jerking and sagging of the capture thread by the spider, resulting (in at least two species) in the prey becoming entangled in one or more loops of sticky thread before the spider arrives to attack.

Second instar spiderlings of *M.* sp. 1 do not disperse, but moult a second time on the surface of the egg sac. Thus they construct webs only after they have fully formed calamistra and cribella and are capable of producing sticky silk. A mature female *M.* sp. 1 constructed nocturnal egg sac webs that were reminiscent of small uloborid orb webs.

The adaptive advantage of the reduced web of *Miagrammopes* is unclear. Many species of small insects are taken as prey and chemical attractants do not seem to be used.

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