

## SHORT COMMUNICATION

### DISPERSAL BY *UMMIDIA* SPIDERLINGS (ARANEAE, CTENIZIDAE): ANCIENT ROOTS OF AERIAL WEBS AND ORIENTATION?

**William G. Eberhard:** Smithsonian Tropical Research Institute, and Escuela de Biología, Universidad de Costa Rica, Ciudad Universitaria, Costa Rica

**Keywords:** Mygalomorph ballooning behavior, orientation

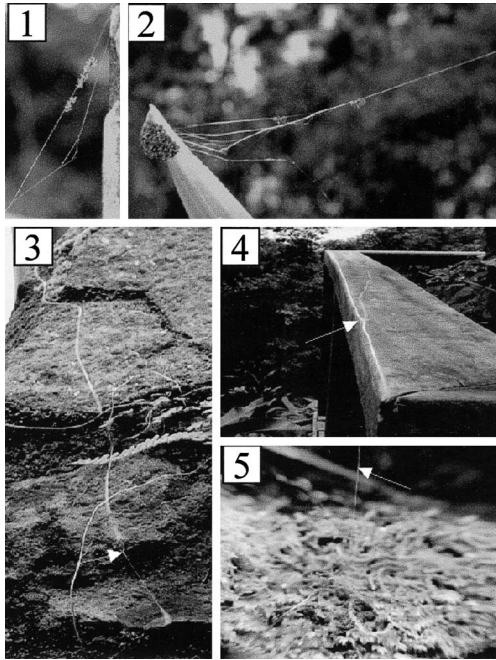
It is well known that many araneomorph spiders disperse by ballooning (e.g. Decae 1987; Suter 1999), but similar dispersal abilities of mygalomorph spiders are much less well established. Previous publications are easily summarized. The most complete observations are those of Coyle (1983, 1985) of spiderlings of *Sphodros* sp. (prob. *S. atlanticus* Gertsch & Platnick 1980) (Atypidae), and *Ummidia* sp. (Ctenizidae). Spiderlings of both species moved along bands of silk lines, and launched themselves into the air after dangling at the ends of draglines. Other descriptions of mygalomorph ballooning did not provide details on how spiders took to the air. Baerg (1928) carefully observed movements of *Ummidia carabivora* (Atkinson 1886) (originally described in the genus *Pachylomerus*) spiderlings from their mother's burrow along wide silk trails to elevated sites, but did not witness the spiders taking off. Enock (1885) saw that *Atypus piceus* (Sulzer 1776) spiderlings followed ascending silken cords to upwardly projecting objects, from which they were "blown off into midair . . . until they became attached to other sticks" (p. 394). Muma & Muma (1945) also observed silk bands produced by the spiderlings of *Sphodros rufipes* (Latrielle 1829) (= *Atypus bicolor* Lucas); they stated that the spiderlings dispersed by ballooning, but gave no details. Cutler & Guarisco (1995) observed a group of spiderlings of *S. fitchi* Gertsch & Platnick 1980 and apparent ballooning attempts at the top of a small tree. Main (1957) suggested that *Conothele malayana* (Doleschall 1859) (Ctenizidae) spiderlings balloon, but only on the basis of observing large numbers of fine threads of silk produced by spiderlings held in collecting tubes. This note reports an observation of dispersal and ballooning by spiderlings of the another ctenizid, an undetermined species of *Ummidia*.

Observations were made in San Antonio de Escazu, San José Province, Costa Rica (el. 1325 m; approximately 9° 51' N, 84° 10' W). Observations with the naked eye were complemented using a 2x

headband magnifier. Some individual silk lines were extremely fine and difficult to see; checks for unseen lines were made by moving an object where a line might have been, and noting whether this movement produced tugs on the spider or nearby silk lines. A voucher (mature female) specimen will be deposited in the Museum of Comparative Zoology, Cambridge, MA 02138, USA.

At about 09:00 on the cool rainy season morning of 17 Oct. 2002 with only intermittent sunshine and weak, erratic wind (a very fine, weak, intermittent drizzle fell briefly at 12:30, but it did not rain until after 15:00), I noted a small ball of spiderlings at the tip of a long thin leaf growing at the edge of the deck of my house (Figs. 1, 2). A file of spiderlings toiled slowly up the edge of the leaf toward the ball. Below the ball of spiders, I traced a more or less straight trail of shiny silk downward along the edge of the leaf, across an open space of about 10 cm to the rock wall supporting the deck, and then across this irregular surface (Fig. 3) for about 70 cm to its end, the edge of the extremely well-camouflaged ctenizid burrow lid covered with green moss (Fig. 5). In places the trail ran along the surface of the wall as a wide band, about the width of a spiderling's body. In others, where it bridged cracks and spaces of up to 7 cm between rocks, it narrowed to a single thick, aerial line (Fig. 3). Spiderlings were scattered along this trail. The burrow entrance was about 10 cm above the ground, in detritus in a shallow indentation in the wall. Spiderlings were emerging one by one from under the lid, which was hinged at the top and slightly open, and climbing up along the trail. Judging by their rates of movement, they must have been emerging for at least 30 min previously. My tentative attempt to lift the lid was answered by a sharp tug that closed and held it tight, showing that the female resident was evidently holding the inner side of the lid (see Bond & Coyle 1995).

The silk trail also continued in the other direction beyond the ball. A few flimsy lines radiated from



Figures 1–5.—Dispersal by *Ummidia* sp. spiderlings. 1. aerial lines to post of railing; 2. spiderling (right) leaves a ball of spiderlings to walk along an aerial portion of the trail; 3. relatively straight silk trail followed by spiderlings across uneven rock face; where the trail was aerial, the band narrowed to a single, thick thread (arrow); 4. horizontal portion of the trail of silk along the top of the railing (arrow indicates fork where some spiders went to the right, others to the left); 5. the trail (single vertical line, arrow) ends on an adult female’s burrow lid, which is camouflaged with green moss.

the tip of the leaf, forming aerial bridges to other leaves 10–20 cm away, and a longer and stronger, approximately horizontal line about 30 cm long connected the leaf tip to the post of the railing of the deck (Figs. 1, 2). From here it ran horizontally along the railing for about 6 m (Fig. 4) until it went straight up the corner of the house for about 4 m to the underside of the roof, where several thin lines bridged to the underside of the eaves. Several lines that streamed downwind from the eaves waved about in the light breeze as if their tips (which I was not sure I could see) were free; the nearest object in that direction was some 10 m away. It is possible that these were lines which had broken when the spider was several m from this takeoff site. An estimated 50–100 spiderlings were seen at different points along the trail during the next two hours, nearly all moving away from the burrow.

The spiderlings dispersed aerially, both from near the ball and from under the eaves. Most of the spi-

derlings in the ball dispersed in the space of 10–15 min around 10:45. No obvious change in wind strength or intensity was noted at this time, but the wind was so light that a subtle change could have gone unnoticed. The last spiderling was seen at about 11:30. In each of five cases in which I observed take-off behavior from the beginning, the spiderling first descended on a dragline that was attached to a horizontal aerial line, and then glided smoothly upward and laterally, moving in the same direction as the wind. The longest glide I was able to follow took the spider just over 5–10 m until the line it was on became entangled in a bush. Another glide, in which I lost sight of the spider when it was about 5 m above the ground, probably took the spider at least 10 m, judging by the direction in which it was moving and the closest objects in that direction.

Much of the spiderlings’ behavior near the ball was apparently tentative. Spiders moved back and forth on the more or less horizontal lines, and ascended and descended vertical draglines. Most descents were followed by ascents of the same line rather than by glides. The draglines were too thin to be easily observed directly, and only occasionally, when lighting and background conditions were appropriate, did I succeed in seeing the silk as the spider descended. Nevertheless, the spider’s movements (slow descent straight downward with the spider facing downward, with its legs more or less spread and moving little if at all; legs never moving as if walking along a line), left no doubt that they were descending at the tips of lines they were producing. The spinnerets were spread, at least in some cases, as the spider descended.

Spiders produced drag lines as they walked along horizontal lines. Some spiders kept their spinnerets spread as they walked, and in these cases it was clear that the spider produced at least two lines, and probably more. When the spinnerets were directed rearward, these lines apparently merged into a single thread. Coyle (1985) reported that each spiderling of *Ummidia* sp. produced a band of numerous fibers as it moved. In no case did I see a spider break and reel up a line as it walked along it (as is typical of araneoid spiders—Eberhard 1982, 1990; Griswold et al. 1998). Nor did a spiderling ever slide tarsus IV along the dragline as it emerged, or break and reel up aerial lines as it moved along them, other traits that are common in araneomorph spiders as they ascend draglines and produce spanning lines (Eberhard 1986, 1987).

I was not able to decipher with certainty how spiders initiated the horizontal aerial lines along which they walked, or the lines with which they ballooned. As in *Sphodros* and *Ummidia* (Coyle 1983, 1985), ballooning was preceded by descent on a dragline. But in no case did the spider give any sign that this dragline broke as it glided up and

away, as described in these other species (Coyle 1983, 1985). The spider's upward and lateral gliding movement was observed carefully: it was very smooth, and was not interrupted by any perceptible jerk that would be produced when a line broke. Nor did the spider move its legs as if reeling in lines, as occurs in some araneomorphs (Eberhard 1987). These details suggest that no lines were broken. It was as if the spider smoothly lengthened its dragline while being pulled by another airborne length of silk.

One long (>1 m) horizontal line was established by a ballooning spider and then used by several other spiders, supporting the idea that at least these early stages of flight during ballooning did not involve breaking the drag line. The new horizontal line ran in just the direction in which the first spider glided away several minutes previously. This line was not present before this spider glided away, because I had walked past this spot several minutes earlier and would have broken any lines there.

In a second case, a line was apparently formed by one spider during the time it hung more or less motionless at the tip of a vertical line. The spider was first observed dangling at the end of a dragline. I passed my hands through the air at its sides and between the spider and my own body without having any effect on its position, thus confirming that there were no unseen lines running from the spider or its dragline in these directions. Nevertheless, in the following minute, during which the spider remained at the tip of its dragline, a line was formed that connected the spider or the dragline near it to my body (perhaps 30 cm away): each time I moved, the spider was displaced. A minute or so later, this spider then glided smoothly away out of sight in a slightly different direction.

These observations of *Ummidia* sp. ballooning are compatible with two different hypotheses regarding the initiation of ballooning lines: the spinneret spreading idea of Blackwell (fig. 1C in Eberhard 1987); and the "second line" method (fig. 2 in Eberhard 1987). It is not clear whether my inability to confirm the third "dragline breaking" technique for initiating ballooning lines, which was proposed by Coyle (1983, 1985) for other mygalomorphs, was due to limitations in the resolution of my observations imposed by my general inability to see the lines the spiderlings were producing, to my inability to follow spiders for longer distances (perhaps they break their draglines after having moved several meters through the air), to differences between species in the process of ballooning, or to imprecisions in previous descriptions. If, as in the observations reported here, the extra ballooning lines (in addition to the dragline) were difficult to see in the *Sphodros* and *Ummidia* species observed by Coyle, his observations are consistent with both the spinneret-spreading and the second line hypoth-

eses, as well as the dragline breaking hypothesis (E. Coyle pers. comm.). Resolution of this uncertainty will unfortunately have to await further lucky occasions when ballooning behavior by mygalomorph spiders can be observed again. Perhaps the most useful technique to employ in such a situation would be to lightly dust the lines with cornstarch or talcum powder, to make additional fine lines visible.

Several details of pre-ballooning dispersal by mygalomorphs merit comment. In both genera that have been observed, the spiderlings migrate as a group from their mother's burrow to the ballooning site, forming a strong band of silk (Baerg 1928, Fig. 3). Spiderlings of the theraphosid *Brachypelma vagans* (Ausserer 1875) also migrate in single file on the ground, perhaps also following a band of silk (Reichling 2000). Such mass movement, and the resulting formation of compact aerial silk highways, is very unusual in araneomorph spiders. I know of only one other case; the highways produced when colonies of the social theridiid *Achaearanea wau* Levi 1982 migrate (Lubin & Robinson 1982). The general pattern for dispersing araneomorphs seems to be for each spiderling to strike out on its own. Spiderlings may benefit from moving as groups; following lines established by nest mates may facilitate rapid movement to ballooning sites.

The ability (and readiness) of *Ummidia* sp. spiderlings to walk upside down along aerial cables (Figs. 1, 2) was surprising. Such dexterity in walking under aerial lines may thus be a very ancient trait, and it could have been important in facilitating the evolution of aerial webs in other groups.

How did these mygalomorph spiderlings orient? Perhaps a partial answer is related to a further remarkable detail of the highways: the trails are quite extraordinarily straight (Figs. 3, 4). Baerg (1928), who observed about 30 different trails of *U. carabivorus* ranging from 10–68 feet long, also noted that trails were "a straight line to the nearest tree of considerable size. A tree less than 6 inches in diameter is usually ignored, even if it is much nearer than some larger tree." Coyle (pers. comm.) has also seen a straight 4 m trail of *Ummidia* across a grassy lawn to the base of a small holly tree. The trail of the theraphosid *B. vagans* may also be relatively straight; the text description says it "snaked its way" along a road, but the accompanying photo shows a straight line of spiderlings (Reichling 2000). If one makes the apparently reasonable assumption that the path of a trail reflects the path followed by the first spiderlings to emerge from the maternal burrow, it seems likely that these animals must have used some sort of landmark orientation or a sun compass to maintain such straight trajectories when crossing irregular terrain, an ability documented in some araneomorphs (Görner 1973, 1986; Tongiorgi 1959). Such an ability is surprising

in spiders that probably seldom venture from their burrows once they are established, and that are generally thought to depend largely on substrate vibrations rather than visual stimuli to orient in other contexts (Coyle 1986). One possibility is that this possibly ancient orientation ability may have evolved to enable males to search more effectively for females, instead of simply wandering randomly (Bell 1991). Male *S. abboti* Walckenaer search for females during the day, and may orient visually toward tree trunks (Coyle & Shear 1981). The searching behavior of mature male mygalomorphs (and for that matter, of mature male spiders in general) seems to be little known, and would repay further study.

I thank Jason Bond for identifying the spider, and Fred Coyle and an anonymous reviewer for many helpful comments on the ms. and references.

#### LITERATURE CITED

- Baerg, W.J. 1928. Some studies of a trapdoor spider (Araneae: Aviculariidae). *Entomological News* 39:1–4.
- Bell, W. 1991. *Searching Behaviour*. New York, Chapman and Hall.
- Bond, J. & F.A. Coyle. 1995. Observations on the natural history of an *Ummidia* trapdoor spider from Costa Rica (Araneae, Ctenizidae). *Journal of Arachnology* 23:157–164.
- Coyle, F.A. 1983. Aerial dispersal by mygalomorph spiderlings (Araneae, Mygalomorphae). *Journal of Arachnology* 11:283–295.
- Coyle, F.A. 1985. Ballooning behavior of *Ummidia* spiderlings (Araneae, Ctenizidae). *Journal of Arachnology* 13:137–138.
- Coyle, F.A. 1986. The role of silk in prey capture by nonaraneomorph spiders. Pp. 269–305. *In Spiders, Webs, Behavior, and Evolution*. (W. A. Shear, ed.) Stanford, CA, Stanford University Press.
- Coyle, F.A. & W.A. Shear. 1981. Observations on the natural history of *Sphodros abboti* and *Sphodros rufipes* (Araneae, Atypidae) with evidence for a contact sex pheromone. *Journal of Arachnology* 9:317–326.
- Cutler, B. & H. Guarisco. 1995. Dispersal aggregation of *Sphodros fitchi* (Araneae, Atypidae). *Journal of Arachnology* 23:205–206.
- Dacae, A.E. 1987. Dispersal: ballooning and other mechanisms. Pp. 348–356 *In Ecophysiology of Spiders* (W. Nentwig, ed.) Berlin, Springer-Verlag.
- Eberhard, W.G. 1982. Behavioral characters for the higher classification of orb-weaving spiders. *Evolution* 36:1067–1095.
- Eberhard, W.G. 1986. Trail line manipulation as a character for higher level spider taxonomy. Pp. 49–51. *In Proceedings of the Ninth International Congress of Arachnology, Panama*. (W. G. Eberhard, Y. D. Lubin & B. Robinson, eds.) Washington, DC, Smithsonian Institution Press.
- Eberhard, W.G. 1987. How spiders initiate airborne lines. *Journal of Arachnology* 15:1–9.
- Eberhard, W.G. 1990. Early stages of orb construction by *Philoponella*, *Leucauge*, and *Nephila* spiders (Araneae: Uloboridae and Araneidae). *Journal of Arachnology* 18:205–234.
- Enock, F. 1885. The life-history of *Atypus piceus*. *Sulz. Transactions of the Entomological Society of London* 1885:389–420.
- Görner, P. 1973. Beispiele einer Orientierung ohne richtende Aussenreize. *Fortschritte der Zoologie* 21:20–45.
- Görner, P. 1986. Adjustment of the optical reference direction in the optical orientation of the funnel-web spider *Agelena labyrinthica* Clerck. Pp. 109–112. *In Proceedings of the Ninth International Congress of Arachnology, Panama 1983* (W. G. Eberhard, Y. D. Lubin & B. Robinson, eds.) Washington, DC, Smithsonian Institution Press.
- Griswold, C.E., J.A. Coddington, G. Hormiga & N. Scharf. 1998. Phylogeny of the orb-web building spiders (Araneae, Orbicularia: Deinopoidea, Araneoidea). *Zoological Journal of the Linnean Society* 123:1–99.
- Lubin, Y.D. & M.H. Robinson. 1982. Dispersal by swarming in a social spider. *Science* 216:319–321.
- Main, B. 1957. Occurrence of the trap-door spider *Conothele malayana* (Doleschall) in Australia (Mygalomorphae: Ctenizidae). *Western Australian Naturalist* 5:209–216.
- Muma, M.H. & K.E. Muma. 1945. Biological notes on *Atypus bicolor* Lucas. *Entomological News* 56:122–126.
- Reichling, S.B. 2000. Group dispersal in juvenile *Brachypelma vagans* (Araneae, Theraphosidae). *Journal of Arachnology* 28:248–250.
- Suter, R.B. 1999. An aerial lottery: the physics of ballooning in a chaotic atmosphere. *Journal of Arachnology* 27:281–293.
- Tongioli, P. 1959. Effects of the reversal of the rhythm of nocturnal illumination on astronomical orientation and diurnal activity in *Arctosa variana* C. L. Koch (Araneae—Lycosidae). *Archivio Italiano de Biologia* 97:251–265.

*Manuscript received 9 September 2003, revised 15 March 2004.*