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Water harvesting during orb web recycling

Brent D. Opell: Department of Biological Sciences, Virginia Tech, Blacksburg, VA 24061 USA; E-mail: bopell@vt.edu

Abstract. Before constructing an orb web, an araneoid spider takes down and ingests the previous day's web. Nocturnal species do this either during the early evening or in the early morning and diurnal species during the early morning, times of the day when relative humidity (RH) is high. Under these conditions the hygroscopic glue droplets of a web's viscous prey capture thread attract atmospheric moisture, providing a net gain of water when a spider ingests its web. The contribution of web recycling to a spider's water budget has been estimated, but not determined empirically. This study does so for adult females of four species (*Araneus marmoreus* Clerck, 1757, *Argiope trifasciata* (Forskål, 1775), *Leucauge venusta* (Walckenaer, 1841), and *Micrathena gracilis* (Walckenaer, 1805)) by first determining the total volume of a web's glue droplets at 20% and 37% RH to estimate the water invested in web during construction. Subtracting each of these values from the web's total droplet volume at 90% RH approximates the range of water harvested when the web is recycled. High estimates of the net water gained range from 0.45% of a spider's body mass (3.01 μl water gained) in *A. marmoreus* to 0.88% of body mass (0.19 μl water gained) in *L. venus*ta. In *A. trifasciata*, the water gained when a web is ingested is equivalent to 29% of a spider's daily evaporative water loss.

Keywords: Evaporative water loss, viscous capture thread, water budget

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Many araneoid orb weaving spiders construct a new web each day. Before doing so, they take down and ingest their existing web (Carico 1986), allowing them to recycle some of the web's low molecular mass compounds and proteins in the next web they construct (Townley & Tillinghast 1988). This adds to the economy of web production and ensures that components, such as choline, which is important for glue droplet hygroscopicity and cannot be synthesized by a spider, are not lost (Townley et al. 2006; Townley & Tillinghast 2013; Jain et al. 2018).

An orb web is composed of frame, radial, and capture threads, with the last comprising both the greatest length and mass (Eberhard 1986). The gluey composite capture thread is the product of three spigots on each of a spider's posterior lateral spinnerets (Coddington 1989). As a flagelliform fiber emerges from a spigot, it is coated with material from two flanking aggregate gland spigots. The strands from each spinneret merge to momentarily form a composite. However, Plateau-Rayleigh instability quickly reconfigures the cylinder into a regular series of droplets (Edmonds & Vollrath 1992; Opell et al. 2018). An adhesive glycoprotein core forms in the center of each droplet and the remaining water, inorganic salts, low molecular mass compounds, and amorphous protein form the thread's aqueous layer, which covers the glycoprotein core as well as the flagelliform fibers in inter-droplet regions (Amarpuri et al. 2015; Jain et al. 2018; Opell et al. 2018).

Compounds that remain in the aqueous layer after a glycoprotein core forms make the droplets hygroscopic and able to attract atmospheric moisture. Consequently, droplet volume tracks environmental humidity, decreasing during the late morning and afternoon hours and increasing during the evening and night. Shortly before constructing an orb web, an araneoid spider takes down and ingests the previous day's web. Nocturnal species do this either during the early evening or in the early morning and diurnal species during the early morning, both times of the day when relative humidity (RH) is high. When a web is taken down and ingested, RH is typically in the range of 90% or greater (Opell et al. 2011a, 2013, 2018; Townley et al. 1991). Thus, in addition to allowing an orb weaver to recycle web protein and droplet solutes, web recycling also provides a spider with water, as the web's fully hydrated capture thread contains more water than the spider initially invested (Edmonds & Vollrath 1992). Edmond and Vollrath reported the water gained to be "about 10% of the spider's daily respiratory water loss", although they did not provide the data and computations behind this assessment.

Therefore, it seemed useful to reassess the importance of orb web recycling to a spider's water budget. The percentage of water in the aggregate material that emerges from a spider's spigots is not known. This might be most accurately determined from material extracted directly from aggregate glands. However, even this would not account for water that might be removed as aggregate material passes down the duct leading to the spinneret. When aggregate material emerges from a spider's spinnerets, it immediately absorbs atmospheric moisture increasing its water content. By desiccating droplets at 20% and 37% RH, I experimentally lowered their water content to levels that I believed approximated that of native aggregate gland material. Subtracting these droplet volumes from those measured at 90% RH and scaling this value to droplet spacing and the length of an orb web's capture spiral estimated the range of net water gained when a spider ingests its web. I computed these values for four orb weaving species whose body masses range from 21 to 677 mg. I also measured the daily evaporative water loss of one of these species, *Argiope trifasciata* (Forskål, 1775), to provide a context for understanding the importance of the water gained during orb web recycling.

METHODS

Species studied.—This study included *Leucauge venusta* (Walckenaer, 1841), the orchard spider, whose horizontal orb webs are found in low vegetation along forest edges; *Micrathena gracilis* (Walckenaer, 1805), the spined micrathe-

Table 1.—Values used to estimate water harvested during orb web ingestion. Spider mass and capture thread length are from Opell (1999) and droplets per mm are from Opell & Hendricks (2009). Sample size is given in parentheses. Values are mean ± 1 standard error.

	Leucauge venusta	*Micrathena gracilis*	*Argiope trifasciata*	*Araneus marmoreus*
Spider mass mg	21 ± 2 (18)	84 ± 5 (21)	474 ± 52 (25)	677 ± 75 (15)
Thread length cm	859 ± 68 (18)	1529 ± 81(21)	2321 ± 173 (25)	2204 ± 139 (15)
Droplets per mm	29.9 ± 2.1 (10)	9.9 ± 1.9 (5)	6.1 ± 0.6 (11)	3.7 ± 0.3 (10)
Droplet features	(13)	(13)	(14)	(14)
Length μm				
20% RH	14.8 ± 0.7	24.7 ± 1.2	51.9 ± 3.6	67.0 ± 2.3
37% RH	16.3 ± 0.8	26.2 ± 1.2	52.2 ± 2.8	69.4 ± 3.0
90% RH	17.4 ± 0.7	31.3 ± 1.5	60.4 ± 3.7	76.9 ± 2.9
Width μm				
20% RH	12.5 ± 0.6	19.6 ± 0.9	37.5 ± 2.7	51.8 ± 2.0
37% RH	13.4 ± 0.7	20.9 ± 0.9	38.5 ± 2.5	54.3 ± 2.8
90% RH	15.1 ± 0.6	25.3 ± 1.2	44.9 ± 2.9	60.9 ± 2.6
Volume μm^3				
20% RH	1,044 ± 141	4,308 ± 580	36,652 ± 7,491	87,258 ± 11,681
37% RH	1,346 ± 193	5,158 ± 593	37,236 ± 6,797	92,468 ± 16,259
90% RH	1,765 ± 194	9,153 ± 1,252	59,245 ± 11,250	123,808 ± 18,247
Droplet volume per mm at 90% RH μm^3	52,774	90,615	361,395	458,090
Droplet uptake μm^3				
37% -> 90% RH	419 ± 146	3,996 ± 984	22,009 ± 6,303	30,232 ± 20,001
20% -> 90% RH	721 ± 153	4,845 ± 984	22,593 ± 5,394	36,918 ± 15,314

na, whose vertical orb webs are found in humid forests; *Argiope trifasciata*, the banded garden spider, whose vertical orb webs are found in weedy vegetation, and *Araneus marmoreus* Clerck, 1757, the marbled orb weaver, whose vertical orb webs are attached to forest edge vegetation. Voucher specimens of these four species are deposited in the Smithsonian Institution's National Museum of Natural History. All capture thread properties were determined from the webs and threads produced by adult female spiders from the same populations living near Blacksburg, Virginia.

Characterizing droplet volumes.—Spider mass and total capture spiral thread length values were taken from Opell (1999) and the number of droplets per mm thread length from Opell & Hendricks (2009) (Table 1). Droplet volumes at 20%, 37%, and 90% relative humidity were newly determined. As in these previous studies, sectors of orb webs were collected on either 18 cm diameter rings or on 15 × 52 cm rectangular frames with double-sided tape (Cat. # 9086K29550360, 3M Co., Maplewood MN, USA.) applied to their 0.6 and 1 cm rims, respectively, to maintain native thread tension. In the laboratory, I transferred capture thread strands to U-shaped brass supports epoxied at 4.8 mm intervals to microscope slides with their upward facing free edges covered with double-sided carbon tape (Cat #77816, Electron Microscope Sciences, Hatfield PA, USA) (Opell et al. 2011b). Capture threads were taken from the outer third of a web and were transferred with forceps whose tips were covered with carbon tape and blocked open to accommodate the spacing of the supports. After pressing the forceps' tips against a capture thread span, I used a hot wire probe or iris scissors to sever the thread's connections to the radii, ensuring that the capture thread was not stretched when it was removed from the web sample.

As described in previous studies (Opell et al. 2013), I placed the microscope slide thread sampler in a glass covered observation chamber that rested on the stage of a Mitutoyo FS60 inspection microscope (Mitutoyo America Corp., Aurora IL, USA) equipped with a Canon Rebel T2i camera. Temperature was maintained at 23° C by a thermostat-controlled Peltier heating/cooling plate attached to the side of the observation chamber. Relative humidity was monitored with a Fisher Scientific Instant Digital Hygrometer model 11-661-7B. A small dish of silica gel desiccant placed in the chamber lowered humidity and a dish with a distilled water-moistened Kimwipe® raised humidity. To precisely maintain the desired humidity levels, small increases in chamber humidity were made by gently blowing in a tube that passed through a flask containing cotton moistened with reverse osmosis "distilled" water and into the chamber. As room humidity was approximately 50% RH, drawing room air into the chamber lowered humidity when it was greater than this value. The precision of this humidity regulation technique is reported in Opell et al. (2013).

Three of an individual spider's droplets were photographed at each RH and their lengths (DL; dimension parallel to the support line) and widths (DW) measured from these digital images using ImageJ (Rasband 1997-2012). I determined the volume of these droplets (DV) using the following formula (Liao et al. 2015) and used the mean of an individual's three droplet volumes in analyses.

$$\mathrm{DV} = \frac{(2\pi \mathrm{x} DW^2 \mathrm{xDL})}{15} \qquad (\mathit{Eq.}1)$$

I converted the mean number of droplets per mm thread length (Opell & Hendricks 2009) to droplets per cm and multiplied this value by the mean length of the capture spiral in a species' web (Opell 1999) to determine the number of glue droplets in its orb web. Total droplet number was then multiplied by a species' mean droplet volume at 20%, 37%, and 90% RH. I estimated the water gained when a spider ingests its web as the differences between 90% RH droplet volumes and its inferred initial aggregate-gland derived water investment, estimated conservatively using 37% RH droplet volume and more liberally using 20% RH droplet volume. I express water gain as both µl of water and as a percent of each species' mean body mass, as determined from spiders whose capture thread lengths were measured (Opell 1999). These volumes do not include the aggregate gland material that covers flagelliform fibers in inter-droplet regions nor the material in very small secondary droplets, which are sometimes found between the large primary droplets (Opell & Hendricks 2009). However, these volumes are much smaller than those of the thread's primary droplets.

Characterizing evaporative water loss.—It is useful to place the water harvested during web recycling in the context of a spider's daily water loss, as Edmonds and Vollrath have done (Edmonds & Vollrath 1992), but this is challenging. Some studies measured the effect of desiccation on spider survival, but do not characterize water loss rates (Hermann & Roberts 2017) and those that do characterize water loss do so under extremely low humidities (Vollmer & MacManon 1974; Markezich 1993) or high temperatures (Davis & Edney 1952), conditions that greatly increase evaporative water loss. Consequently, there appear to be no baseline values for orb weaving spiders under conditions similar to those they experience in nature. To provide this perspective, I gathered data on evaporative water loss in *A. trifasciata*.

I collected 20 adult female *A. trifasciata* from weedy vegetation on the edge of Virginia Tech's campus on 2 October 2019 and placed each in a 120 ml, 7 cm high, 4.5 cm diameter cylindrical plastic container with the lid resting loosely on top. A ball of cotton wetted with reverse osmosis "distilled" water and a damp paper towel in the container provided the spider with water and maintained a high container humidity during the four days that these spiders were allowed to become fully hydrated, acclimate to laboratory conditions, and clear their digestive systems. During this time and for the remainder of the experiment, a 13-hour light–11-hour dark cycle was maintained. At the end of the fourth day, I weighed each spider with an American Scientific DTL 350s balance, which has a resolution of 1 mg, removed the cotton and paper towel from the spider's container, cleaned the container with 100% ethanol on a Kimwipe®, and returned the spider to its original container. To ensure ventilation, I then covered the container with cheesecloth held in place with a rubber band.

For the next three days, temperature and RH were recorded every 15 minutes with an Onset Hobo U23 Data Logger, which registered a mean temperature of 20.7° C ± 1 standard deviation of 0.4° C (range: 20.3 – 22.2° C) and a mean RH of 57.5% ± 1.3% (range: 53.3 – 60.3%). This was similar to the grand mean temperature of 21.2° C recorded at Virginia Tech's three Blacksburg area weather stations (Campus, Drone Park, Kentland Farms) from 20 August – 30 September 2019 (online at https://montgomery.weatherstem.com/vt), the time period during which most *A. trifasciata* mature and produce egg sacs (Opell, pers. obs.). However, laboratory RH was lower than the grand mean of 75% recorded by the weather stations. Thus, measured evaporative water loss was higher than these spiders would have naturally experienced, although some of difference may have been offset by the fact that spiders' confinement constrained their activity and by their lack of exposure to wind and sunlight.

I reweighed the spiders on the following three days with median times of 23.70, 24.08, and 23.68 hours separating their weights. During this time two spiders defecated, one lost a leg, and one died, leaving 16 individuals for which I obtained a series of three reliable weights. Two tailed matched paired tests showed no differences among weight lost during the three time periods ($P = 0.1317 - 0.3792$). Therefore, I computed each spider's average hourly weight loss over the entire 71.63-hour observation period and multiplied this value by 24 to determine its average daily weight loss, which I equate with a spider's evaporative water loss. The 19 spiders alive at the end of the study showed no ill effects of confinement, remaining responsive and mobile, readily climbing plant stems when returned to their collecting sites.

RESULTS

The total volume of an orb web's capture thread droplets is quite small in comparison with a spider's mass (Table 1, Fig. 1). Consequently, the potential for this web component to contribute to a spider's water budget is limited. Estimates of net water gain range from a high of 0.88% of body mass (0.19 µl water harvested) in *L. venus*ta to a low of 0.45% of body mass (3.01 µl water harvested) in *A. marmoreus*. A sample size of four species does not support a robust statistical or phylogenetic analysis. However, a comparison of these species' values suggests that, relative to spider mass, the net water gained from web ingestion decreased as spider mass increased (Fig. 2a,b). This was the case despite larger spiders having proportionately longer capture spirals (Fig. 2c). The percent droplet volume increase from 20% to 90% RH was normally distributed for each species (Shapiro-Wilk W Test $P = 0.14 - 0.52$) and did not differ among species (ANOVA $P = 0.1748$), but paired t-tests showed that the extreme values of *M. gracilis* and *A. marmoreus* were different ($P = 0.0344$).

The 16 *A. trifasciata* included in the evaporative water study had a mean mass of 581 mg ± 1 standard deviation of 233 mg, an hourly water loss of 0.53 ± 0.27 µl, and a 24-hour water loss of 12.73 ± 6.42 µl, which was 2.29 ± 1.00 % of the spider's initial mass. A linear regression of spider mass and water loss (Fig. 3) was significant ($P = 0.0208$), though not robust ($R^2 = 0.33$). However, it allowed the daily evaporative water loss of a 474 mg individual, the mean size of spiders on which this species' capture thread length was determined (Opell 1999), to be inferred as 11.05 µl using the following equation.

$$\text{Water loss in } \mu\text{l per 24 hours} = 0.01576 \text{ mass in mg} + 3.5769 \quad (2)$$

If a spider of this size obtained a maximum net water gain of 3.20 µl from web ingestion (Fig. 1), this would be the equivalent of 29% of its daily evaporative water loss, as measured in this study.

DISCUSSION

Images of spider orb webs glistening with morning dew are familiar and have inspired human efforts to harvest water from the environment (e.g., Bai et al. 2012; Brown & Bhushan 2016; Zhu et al. 2016; Tian et al. 2017). Although a spider can

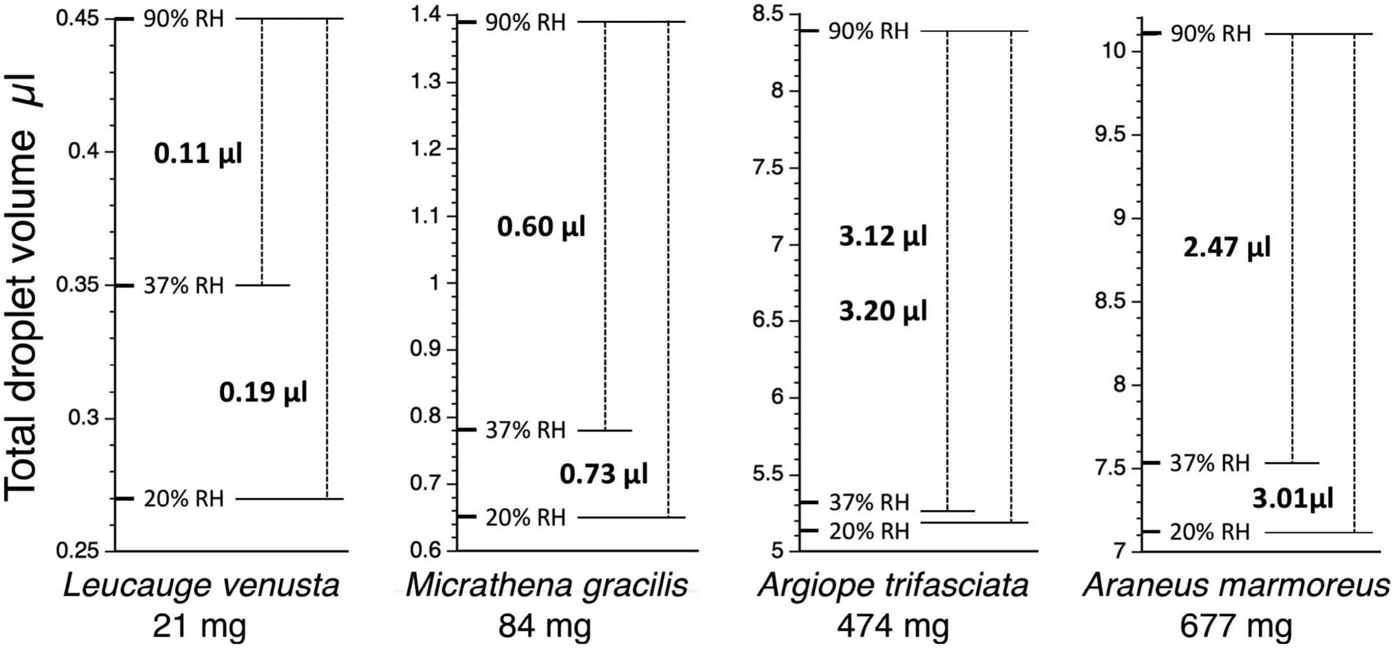

Figure 1.—Total droplet volume per orb web at three relative humidities (RH) and the water gained during web recycling in bold numbers. For each species the larger, lower water volume value is the difference between 90% and 20% RH values and the smaller, upper value is the difference between 90% and 37% RH values.

drink water that has condensed on its web strands and stabilimentum during these times (Walter et al. 2009, 2011, 2012), it gains less water from web recycling than these web photographs might suggest. In the four species examined, the water gained amounts to less than 1% of a spider's mass. However, when viewed from the perspective of water lost through evaporation from an orb weaver's book lungs, trachea, and body surface, web recycling does make a significant contribution to a spider's water budget. This source is equivalent to almost a third of *A. trifasciata*'s evaporative water loss, an amount greater than previously reported (Edmonds & Vollrath 1992).

Droplet size, spacing, and hygroscopicity combine with capture spiral length to determine the amount of water that a spider can obtain when it ingests a web. The capture threads of small spiders have more closely spaced droplets than do those of larger spiders. However, this does not compensate for the small size of droplets along capture threads spun by smaller spiders. Consequently, at 90% RH, the total droplet volume per mm capture spiral length increases greatly with spider size (Table 1).

These estimates of the water gained during web recycling and the contribution of this activity to a spider's water budget may be conservative for several reasons. Although a RH of 20% is much lower than that naturally encountered by members of these four species, at this humidity glue droplet water content may still exceed that of the aggregate gland material issuing from a spider's spinnerets. The inability of *A.*

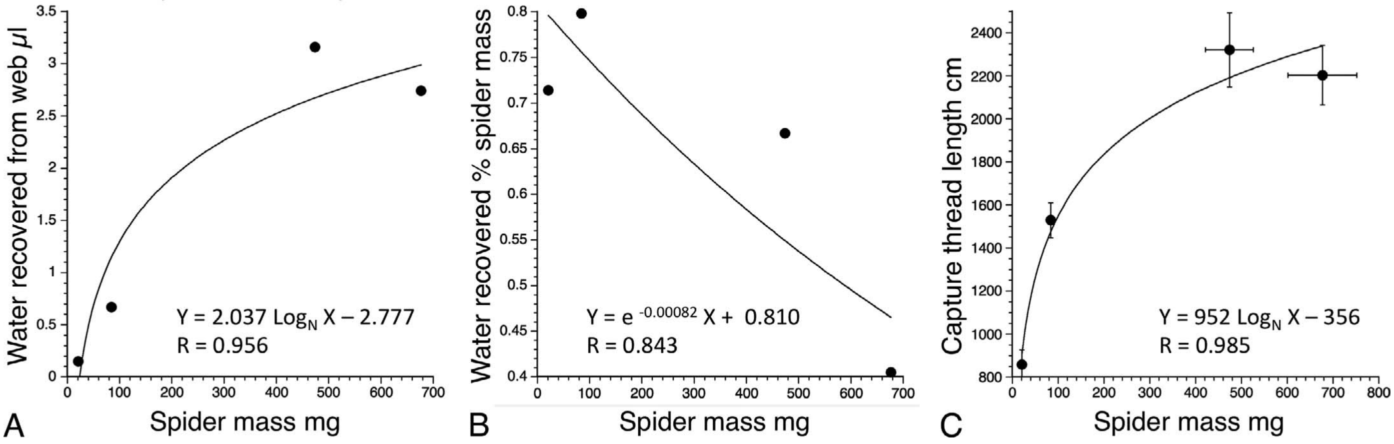

Figure 2a–c.—Relationships between spider mass and net water gained during web recycling (a), net water gained as a percent of spider mass (b), and capture thread length per orb web (c) for the four species studied. Standard errors are provided only for spider mass and thread length (c) because the values used to compute water gained are the product of values from studies of different individual spiders.

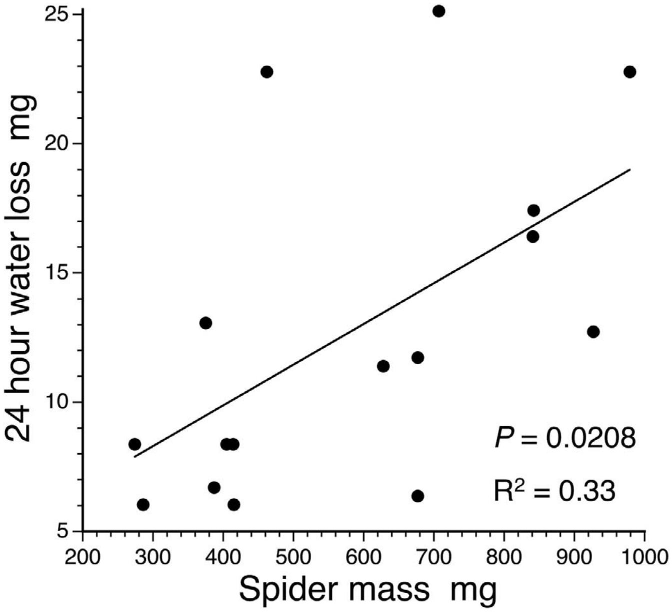

Figure 3.—Regression of initial spider mass and mean daily evaporative water loss in 16 adult female *Argiope trifasciata*. The regression line is described by the formula: Y = 0.01576 X + 3.5769.

trifasciata to construct webs during their confinement lowered their metabolic rates and related respiratory water loss. However, the lower humidity of experimental conditions when compared to these spider's natural habitat almost certainly overshadowed this difference to produce greater respiratory water loss and, hence, a more conservative estimate of the importance of web recycling to the water budget of *A. trifasciata*. However, the contribution of web recycling to *A. trifasciata* water budget may be greater than in other large orb weavers because this species is resistant to desiccation, as suggested by a comparison with *Argiope aurantia* Lucas, 1833 (Markezich 1993). By virtue of its large size, *A. trifasciata* has a smaller surface to volume ratio than do the smaller *L. venusta* and *M. gracilis* included in this study. Therefore, it is possible that web recycling may make an even greater contribution to the water budgets of small orb weavers.

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