

An Immense Concentration of Orb-Weaving Spiders With Communal Webbing in a Man-Made Structural Habitat

[Arachnida: Araneae: Tetragnathidae, Araneidae]

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In late October, 2009, the managers of the Back River Wastewater Treatment Plant in Baltimore, MD sought assistance in mitigating what they described as an “extreme spider situation” in their sand filtration facility. The building, consisting of almost four acres (16,099 m²) under a single roof but with no side walls, had been prone to extensive colonization by orb-weaving spiders since its construction in 1993. However, the present infestation was considered to be worse than normal, and the facility’s maintenance and operations personnel had voiced concerns over the potential risk of bites.

As an interagency team with expertise in arachnology, urban entomology, and structural pest management, we were unprepared for the sheer scale of the spider population and the extraordinary masses of both three-dimensional and sheet-like webbing that blanketed much of the facility’s cavernous interior. Far greater in magnitude than any previously recorded aggregation of orb-weavers, the visual impact of the spectacle was nothing less than astonishing. In places where the plant workers had swept aside the webbing to access equipment, the silk lay piled on the floor in rope-like clumps as thick as a fire hose.

This report has three objectives: 1) to document the phenomenon, providing photographs, species determinations, and estimates of the total extent of web construction and numbers of spiders involved; 2) to compare this remarkable concentration of normally solitary orb-weaving spiders with similar megawebs reported from both anthropogenic and non-anthropogenic habitats, as well as to review the range of antecedents for this behavior; and 3) to emphasize the potential research utility of aquacentric structures such as sewage treatment plants as readily accessible “culturing facilities” for predictable, dense aggregations of these spiders.

Materials and Methods

Study Site. The Back River Wastewater Treatment Plant is owned and operated by the City of Baltimore and is situated on the west shore of Back River, a tributary of the Chesapeake Bay. Its sand filtration facility serves as a final “polishing” step in the purification

process by trapping the remaining suspended particles from the wastewater. The building houses a total of 48 rectangular sand beds, each measuring 35.36 m x 4.88 m, arranged perpendicularly on either side of a tall central corridor that is aligned north-south (Fig. 1). Both sides of the facility are nearly identical, and are each covered with a low-slope roof supported by rows of steel columns. As is common in pre-engineered metal buildings, these columns are fastened to transverse I-beams (rafters) that support purlins running the long axis of the structure. Whereas the average height of the side roofs is about 4.0 m, the central corridor’s roof is about 7.5 m at its peak. The primary purpose of designing the facility with a roof was simply to minimize algal growth in the sand beds, which would decrease their filtration capacity and increase the frequency of cleaning.

Web Samples. The two principal types of webbing throughout



Fig. 1. Back River sand filtration facility, central corridor.



Fig. 2. Cutting sample of laminar webbing from ceiling with pole pruner saw.

the structure will be referred to as volumetric (a tangled, three-dimensional mass) and laminar (a thin, dense sheet), and are described in more detail in the text. Observations, photography, and collection of web samples took place from 11:00 a.m. to 4:00 p.m. on 6 November 2009. Twelve 2.36 m x 3.0 m sections of laminar webbing were cut with a pole pruner saw from the nearly continuous sheet of silk below the ceiling of the side roofs (Fig. 2). Four of the samples were from the facility's west side, and eight were from the east side. The sheet thickness varied from about 0.5 to 1.0 cm; the volume of each laminar sample, assuming a standard thickness of 0.75 cm, was therefore 0.0531 m³. (This parameter was expressed as 4 digits for both sets of samples in order to yield the most conservative values for spider densities.)

Samples of volumetric webbing were scooped with a piece of fitted cardboard from the space between the flanges of six steel columns throughout the facility, three on either side of the central corridor. Each sample consisted of a 2.0 m length of column, starting at the floor. The space between the flanges was 0.20 m wide and 0.08 m deep, so the volume of each column sample was 0.0320 m³.

All webbing samples were bagged and refrigerated, and their spider occupants were extracted by hand and preserved in 70% ethanol. Specimens are deposited in the United States National Museum (USNM), Washington, D.C.

Estimation of Total Web Area, Volume, and Spider Population.

Since the sand filtration facility is a modular structure consisting of various repeating architectural units, rough estimates of the total number of spiders present could be made by first calculating the extent of laminar and volumetric webbing throughout the building, and then extrapolating from the species composition within the analyzed web samples. Both architect's drawings provided by the plant managers and on-site measurements were used to parse the facility into its structural components. Over 300 photos were used as an aid to derive the percentages of these components that were covered or filled by webbing on the sampling date. See text for further discussion of the assumptions and limitations of the estimation process.

Following are the architectural units used to establish the webbing estimates:

Ceiling Above Sand Beds. Each low-slope roof on either side of the central corridor measures 181.31 m long and 41.86 m wide, with a total combined area of 15,179.27 m². In calculating the amount of laminar webbing covering the ceiling beneath these roofs (Fig. 3), it was necessary to first subtract the summed footprints of the 26 sets of trolley beam hangers (described below), a separate structural component that formed the supports for the facility's most conspicuous masses of volumetric webbing. The area of each rectangular footprint for a row of hangers is 104.07 m². Without them, the remaining ceiling surface is 12,473.45 m².

Roof Support Columns. The building's roof is supported by 27 transverse rows of "wide flange" steel columns, each row comprising five columns on either side of the central corridor. The channels between the flanges of almost every column were completely filled with webbing (Fig. 4). All channels are 0.08 m deep, but there are three different widths. The outermost columns of each row are 0.30 m wide; the three middle columns of each set of five are 0.20 m wide; and the innermost columns that support the central corridor's roof



Fig. 3. Laminar webbing covering ceiling (right side of photo), grading into volumetric webbing between trolley beam hangers (left side of photo).

are 0.25 m wide. Each category of column also has a different length: the outermost ones are 3.05 m tall; the three middle ones vary due to the sloping side roofs and have a mean height of 3.35 m; and the innermost ones are much taller, with a height of 7.11 m.

Trolley Beam Hangers. The trolley beam hangers are rows of rectangular steel frames, fastened to the roof purlins between every other sand bed, that support the horizontal beams holding the sliding loops of electrical cables for the traveling bridges. Each side of the facil-



Fig. 4. Spiders in web-filled flange column.



Fig. 5. Webbing inside row of trolley beam hangers.



Fig. 6. Closeup of trolley beam hanger webbing. The black specks are mainly individuals of both *T. guatemalensis* and *L. sclopetarius*.

ity has 13 rows of 19 hangers. Many of these rows served as the framework for a three-dimensional, roughly rectangular mass of webbing 39.42 m long, 2.64 m wide, and an average of 1.27 m high (Figs. 5 and 6).

Influent Channels. Grated catwalk-covered channels carrying the influent wastewater from the previous stage in the purification process are located between every other sand bed, totaling 12 on each side of the facility. Most of these channels, measuring 41.86 m x 2 m x 1 m to water level, were completely filled with webbing (Fig. 7), including the catwalk grate openings.



Fig. 7. Webbing beneath catwalk in influent channel. The black specks are mainly individuals of *L. sclopetarius*.



Fig. 8. Webbing beneath traveling bridge.

Traveling Bridges. Each sand bed is serviced by a traveling bridge containing a backwash pump that pulls up the entrapped solids as the structure slowly moves on side rails over the bed. The particle-laden water is then pumped back for re-treatment at an earlier stage in the purification process. The space between the bridge deck and its hanging boom, measuring 4.88 m x 1.68 m x 1.17 m, was typically filled with webbing (Fig. 8).

Railings. The extensive safety rails in the facility served as webbing frameworks throughout much of their lengths (Fig. 9). Six rows of railings measuring 181.31 m x 1.07 m x 0.05 m parallel the building's long axis: one on either side of the central corridor and one on either side of the narrow walkway on both outer edges. Although the inner railings had gaps to allow access to the transverse catwalks, they are treated as continuous lengths because the spiders readily webbed across them. In addition, each of the traveling bridges had a pair of railings, each measuring 6.10 m x 1.09 m x 0.05 m.

Electrical Conduits. Two parallel tracks of electrical conduit run along either side of the central corridor and served as webbing frameworks in the same manner as the safety rails. Each set of conduits measures 181.31 m x 0.42 m x 0.13 m.



Fig. 9. Midges in webbing between safety rails. Many of these individuals are resting on non-sticky threads.



Fig. 10. Partially detached sheet of webbing (about 6.5 m across) from beneath ceiling.

Results

Webbing. The most distinctive manifestation of the spider population inside the sand filtration facility was the enormous mat of webbing that obscured about 70% of the ceiling on either side of the central corridor; a mostly unbroken expanse of relatively dense, uniformly thick (about 0.5 to 1.0 cm) silk that covered a total area of about 8,731.42 m². The sheet was anchored principally to the purlins (horizontal roof supports running the long axis of the building) and rafters (larger, transverse beams that support the purlins), rather than to the underside of the roof itself. On 29 October, when A.G. and N.L.B. first observed the site, this laminar web was intact over an even greater percentage of the ceiling. By the sampling date of 6

Table 1. Architectural Elements Used to Estimate Total Amount of Volumetric Webbing in Back River Sand Filtration Facility.

Feature	Unit Volume (m ³)	No. units	Estimated Percentage total volume occupied by webbing	Total webbing volume (m ³)
Inner Flange Columns	.28	54	95	14.36
Central Flange Columns	.10	162	95	15.39
Outer Flange Columns	.14	54	90	6.80
Trolley Beam Hangers	132.17	26	60	2,061.85
Influent Channels	83.72	24	80	1,607.42
Traveling Bridges	9.59	48	80	368.26
Traveling Bridge Railings	.33	96	90	28.51
Corridor & Side Railings	9.70	6	70	40.74
Electrical Conduits	9.90	2	95	18.81

November, sections up to 6.5 m across had begun to separate from their narrow attachment points (Fig. 10), primarily toward the edges of the building due to wind from a recent storm.

Similarly, what had apparently been more extensive laminar webbing across the central corridor ceiling earlier in the season had undergone cycles of sectional fraying and reattachment, so that in places the silk sheets resembled wash hanging on lines in an alley (Fig. 11). Measured directly, the combined area of these remnants was approximately 191.0 m². Together with the main horizontal expanses under the side roofs, the total laminar webbing in the building was about 8,922.42 m².

However, the majority of webbing throughout the facility was volumetric, occupying a total space of approximately 4,162.14 m³. Table 1 lists the various architectural units that had been used as supports for these masses of tangled silk strands, and the estimated extent of their combined volume that was filled with webbing on 6 November. By far the principal component of the total output was the 26 rows of trolley beam hanger webbing, producing much of the immediate visual spectacle of the phenomenon. In contrast, the second largest component was the 24 influent channels, the web-filled interiors of which were out of sight beneath grated catwalks.



Fig. 11. Sections of laminar webbing beneath central corridor ceiling.

Despite being abundantly occupied with spiders, the webbing in most locations was dense enough to catch most of their excreta, leaving the floors, catwalks, and other lower surfaces largely free of this material. Although much of the volumetric silk had the same seemingly haphazard structure of cobweb, these networks—particularly the more extensive and readily visible ones supported by the trolley beam hangers, traveling bridges, and railings—nevertheless also displayed conspicuous sheet-like organization to their construction (Figs. 5, 6, and 8). In addition, small complete or partial orb webs could occasionally be discerned amidst the sparser tangles, particularly where *Larinioides* was more abundant.

Although, for the sake of convenience, the calculations of webbing dimensions assumed a strict spatial

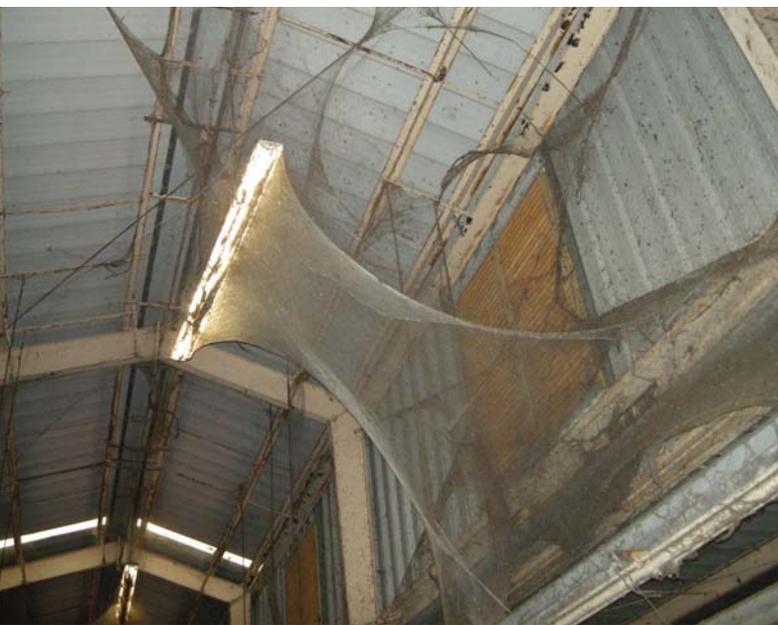


Fig. 12. Hanging 8' light fixture (2.44 m long) pulled out of alignment by webbing.

discontinuity between laminar and volumetric production, their boundaries in reality were usually imprecise. For example, the expanse of webbing conspicuously pulling an 8' overhead light fixture (2.44 m long) out of alignment (Fig. 12) was recorded as part of the central corridor ceiling's laminar total, even though its sheet-like component graded into a three-dimensional mass. In addition, the various units of volumetric silk typically extended beyond the structural frameworks used to calculate their volume (Fig. 3). The webbing was therefore essentially continuous throughout the building, often with extensive bridging between our arbitrarily delineated categories. For these reasons, our estimates of its total extent are markedly conservative and represent what we regard as minimum values.

All webbing decreased to some extent toward the facility's exposed periphery. By 14 December, its reduction throughout the entire building was considerable. Both laminar and volumetric silk had become tattered and fragmented in virtually every location, supporting the plant managers' observations that the webbing recorded on the sampling date was almost entirely the result of a single season's work. However, web construction in the facility continued at a low level throughout the winter. On 22 February 2010, small amounts of fresh silk in the form of accumulated drag lines and tangled volumetric webbing, often with a strong laminar component, were locally conspicuous on posts, railings, and cavities in equipment, all in association with adult female *Larinioides* that were sheltering nearby (see following section).

Spiders. A total of 31,194 specimens, 24,171 of which were hatchlings, were extracted from the web samples. Although 9 genera in 6 families were represented (Table 2), the webbing was almost entirely the product of two hyperabundant species, *Tetragnatha guatemalensis* O. Pickard-Cambridge and *Larinioides scolopetarius* (Clerck), which respectively comprised 63.4% and 21.6% of the non-hatchling sample of 7,023 individuals. All hatchlings were *T. guatemalensis*, further contributing to the pronounced dominance of this species at the site. Since these tiny spiderlings began actively dispersing as soon as the web samples were removed from their bags, many escaped capture and their actual number substantially exceeded our total. In fact, the aggregation as a whole at the time of sampling was overwhelmingly one of immatures. Even if the hatchlings are ignored, juveniles composed 84.4% of the collected specimens, with the percentages for the two principal species virtually identical at 83.2% (*T. guatemalensis*) and 83.1% (*L. scolopetarius*). This extremely close similarity was repeated with the sex of the adult specimens, which were 68.9% female for both *T. guatemalensis* and *L. scolopetarius* (Table 2).

As might be expected, the spider populations were not uniformly distributed throughout the facility, but displayed considerable differences both between and within the two data sets of ceiling and column samples. Of the four principal species, densities of non-hatchling *T. guatemalensis*, *L. scolopetarius*, and *Parasteatoda tepidariorum* (C. L. Koch) were far greater in the volumetric webbing of the column samples (Table 3). However, mean density of *T. guatemalensis* hatchlings in the ceiling web sheet was almost 4x their density in the column webbing (Table 3), at least in part due to the females' tendency to deposit their egg sacs above the areas of greatest spider activity. Although many of the sacs were in the sheet itself, the disintegration of most of the webbing in the winter revealed that thousands had been deposited on ceiling supports and other overhead fixtures. *Dictyna bellans* Chamberlin was also heavily concentrated in the ceiling sheet by a factor of 10 (Table 3).

In addition, at least some of the preponderance of *L. scolopetarius* in the volumetric webbing might have been due to a sampling artifact. Adults of this species typically spend the daytime resting in a concealed location off their web, including structural cracks and crevices (Levi 1974, Burgess and Uetz 1982, Uetz 1986, Dondale et al. 2003). When the site was first observed on 29 October, conditions were extremely overcast and numerous adult and sub-adult *L. scolopetarius* were visible in both the volumetric and laminar webbing throughout the facility. In contrast, the weather was sunny on the sampling date of 6 November and many of these individuals were withdrawn from the webbing and quiescent against the adjacent

Table 2. Numbers of spiders collected in webbing samples from Back River Sand Filtration Facility.

Family	Species	♂	♀	Juveniles	Total
Araneidae	<i>Larinioides scolopetarius</i> (Clerck)	80	177	1,262	1,519
	<i>Mangora</i> sp.			1	1
Dictynidae	<i>Dictyna bellans</i> Chamberlin	6	52	604	662
Gnaphosidae	Gnaphosidae sp.			1	1
Salticidae	<i>Sitticus fasciger</i> (Simon)	3	7	12	22
Tetragnathidae	<i>Tetragnatha guatemalensis</i> O. P-C.	232	515	3,705	4,452
	<i>T. guatemalensis</i> hatchlings				24,171
Theridiidae	<i>Parasteatoda tepidariorum</i> (C. L. Koch)	3	17	338	358
	<i>Steatoda grossa</i> (C. L. Koch)	1			1
	<i>Steatoda triangulosa</i> (Walckenaer)	1	2	2	5
	Theridiidae sp.			2	2
Totals		326	770	5927	31,194

Table 3. Densities of the 4 most abundant spider species in the Back River Sand Filtration Facility, expressed as numbers of individuals per m³ (mean and range), from volumetric (flange columns) and laminar (ceiling sheet) webbing samples. See text for additional details.

Species	Volumetric	Laminar
<i>Tetragnatha guatemalensis</i> O. P-C., hatchlings	9,151 (1,594 – 24,063)	35,176 (1,601 – 136,535)
<i>T. guatemalensis</i> , non-hatchlings	9,917 (4,031 – 17,750)	3,999 (1,375 – 9,454)
<i>Larinioides sclopetarius</i> (Clerck)	4,500 (3,469 – 5,438)	1,028 (264 – 4,765)
<i>Parasteatoda tepidariorum</i> (C. L. Koch)	1,380 (563 – 2,156)	146 (0 – 452)
<i>Dictyna bellans</i> Chamberlin	99 (0 – 219)	1,009 (94 – 3,955)

structural elements. Large specimens of *L. sclopetarius* in webbing were only plentiful in the darkness beneath the catwalks of the influent channels (Fig. 7). Whereas the scooping of the volumetric webbing from between the column flanges was able to capture the *Larinioides* appressed against the column shafts, such individuals were naturally excluded from the ceiling sheet samples. However, since juvenile *L. sclopetarius* may remain in their webs during the daytime (Wiehle 1931, cited in Dondale et al. 2003), the overall significance of the undercounting is unknown.

Both types of webbing included one or a few samples containing atypically dense spider concentrations. Different species usually displayed extreme local abundance in different locations; only the maximum ceiling sheet densities of *L. sclopetarius* and *D. bellans* occurred in the same sample (which respectively contained 38.6% and 32.7% of the ceiling totals for these two species). The sheet webbing in particular varied considerably from place to place, some samples consisting primarily of apparently newer, cleaner silk and others packed with the remains of prey and associated dermestid larvae. However, condition of the webbing was not correlated with maximum or minimum spider numbers.

In contrast to normalizing the specimen counts as densities, calculating total populations of spiders present in the sand filtration building by applying these counts to the total estimated amounts of volumetric and laminar webbing throughout the facility (see previous section) produced a somewhat different view of the aggregation.

Table 4. Estimated populations of spiders in the Back River Sand Filtration Facility, based on numbers of individuals from volumetric (flange columns) and laminar (ceiling sheet) webbing samples applied to an estimated 4,162.14 m³ of volumetric webbing and 8,922.42 m² of laminar webbing. See text for additional details.

Species	Volumetric	Laminar	Total
<i>Tetragnatha guatemalensis</i> O. P-C., hatchlings	38,087,915	2,353,896	40,441,811
<i>T. guatemalensis</i> , non-hatchlings	41,274,554	267,588	41,542,142
<i>Larinioides sclopetarius</i> (Clerck)	18,729,629	68,787	18,798,416
<i>Parasteatoda tepidariorum</i> (C. L. Koch)	5,744,620	9,767	5,754,387
<i>Dictyna bellans</i> Chamberlin	411,878	67,527	479,405
Other species	260,134	2,100	262,234

Since the amount of volumetric webbing in various locations (Table 1) was so much greater than the ceiling sheet webbing, estimated numbers of hatchling and non-hatchling *T. guatemalensis* on a habitat-wide basis were quite similar (Table 4). Total numbers of spiders living in the facility on 6 November were estimated as 40.4 million *T. guatemalensis* hatchlings and 66.8 million non-hatchlings of all species (Table 4).

Discussion

Communal Behavior By Solitary Orb-Weaving Spiders. Although the construction of a spider web, and particularly an orb web, has often been regarded as a rigidly constrained series of steps yielding a stereotyped product (Shear 1986), a major subset of arachnological research continues to demonstrate that the process is often highly plastic and the end result potentially quite variable (Heiling and Herberstein 2000, Blackledge and Zevenbergen 2007, Salomon 2007). Similarly, despite the frequent generalization of spiders as territorial and cannibalistic (Wise 2006), a considerable range of aggregative behavior has been recorded in which conspecific and even heterospecific individuals of typically solitary species closely coexist with minimal aggression and the blending of web boundaries (Whitehouse and Lubin 2005, Salomon 2007). These two spectra of web variability and tolerance for neighbors have repeatedly been shown to overlap, up to the extremes for both behaviors illustrated by the Back River spider community and similar giant conspecific and heterospecific webs observed in both structural and non-anthropogenic habitats (Burgess and Uetz 1982, Uetz 1986, Leech 2003, Quinn 2007, Jackman et al. 2007).

Since increased foraging success appears to be the evolutionary driver for much of spider sociality (Whitehouse & Lubin 2005), it is unsurprising that local prey abundance frequently appears to be the basis for facultative aggregating behavior by otherwise non-social species, although several factors relating to conspecific attraction may also be responsible (Burgess and Uetz 1982, Rypstra 1985, Leborgne and Pasquet 1987, Gillespie 1987b, Lloyd and Elgar 1997, Heiling 1999, Schuck-Paim and Alonso 2001). Interestingly, the general correlative rule between prey availability and an individual spider's silk production differs according to the species' web design. Three-dimensional builders with energetically costly, persistent webs that are continually repaired and expanded have been shown to increase web size and/or density when well fed (Roush and Radabaugh 1993, Segoli et al. 2004, Blackledge and Zevenbergen 2007, Salomon 2007), perhaps in part due to an increased ability to allocate more energy towards protection from predators (Blackledge et al. 2003). In contrast, orb-weavers with ephemeral webs that are frequently recycled by ingestion build smaller orbs and/or display a lower incidence of web construction under conditions of excess prey and satiation (Gillespie 1987b, Sherman 1994, Pasquet et al. 1994, Tso 1999, Herberstein et al. 2000, Thévenard et al. 2004).

The proximity of neighbors in favorable habitat patches adds another, often even more significant, variable to orb web dynamics. Depending on species and circumstances, close spacing of individuals may result in an increase in conspecific and heterospecific competitive web invasions (Enders 1974); construction of smaller orbs by late-arriving individuals, with few webs having threads in common (Leborgne and Pasquet 1987); the opposite phenomenon of an increase in inter-orb attachments (Rypstra 1985, Lloyd and Elgar 1997); and the even more extreme occurrence of communal, non-orb silk used indiscriminately by all individuals for prey capture (Gillespie

1987b). (All of these examples involve what have been referred to as “fortuitous aggregations of individuals of solitary species” [Uetz and Hieber 1997] and exclude the approximately 60 “colonial” and “social” spider species that either commonly or invariably live in groups [Uetz and Hieber 1997, Whitehouse and Lubin 2005].)

Species in the widespread orb-weaving genera *Larinioides* and *Tetragnatha* are solitary spiders that are frequently abundant near aquatic habitats such as the margins of rivers and lakes. *Larinioides* spp. often attach their webs on anthropogenic structures, particularly near lights. The adults are nocturnal, constructing simple vertical orbs with relatively few radii and support strands in the evening, remaining at the hub until morning, and withdrawing either to the web periphery or a silk retreat during the day (Levi 1974, Dondale et al. 2003). The holarctic *L. sclopetarius* (probably introduced to North America, cf. Ware and Opell 1989) is an especially synanthropic spider that is strongly associated with water and actively chooses locations illuminated by artificial light (Heiling 1999). Favorable sites may be occupied by crowded populations of this species, often with inter-web attachments and shared web boundaries (Wąsowska 1973, Heiling 1999, Howes 1999, Dondale et al. 2003). Observations on an aggregation of over 250 adults and sub-adults on the metal framework of an aqueduct revealed that the spiders “readily moved from web to web when disturbed without obviously exhibiting aggressive behaviour to their neighbours” (Howes 1999).

However, the most extreme recorded example of conspecific tolerance and collective silk in *L. sclopetarius* was a significant departure in scale from the above observations, involving an enormous, recurring population on the Riverfront Coliseum Sports Arena in Cincinnati, OH (now known as the U. S. Bank Arena), apparently as an aggregative response to abundant prey from the adjacent Ohio River. Densities of 100 spiders/ m³ were observed on masses of webbing that apparently resulted from collapsed orbs and common attachment strands. The spiders maintained their normal activity cycle, capturing insects and mating on the communal silk during the night and packing into building crevices during the day (Burgess and Uetz 1982, Uetz 1986). A similar example of local hyperabundance of the closely related *L. patagiatus* (Clerck) was observed in a power plant wheelhouse, consisting of “thousands of juxtaposed webs and an estimated 10,000 to 20,000 spiders of all life stages sharing the webs almost communally” (Leech 2003). A photograph included in this account shows a distinct, sheet-like integration of the accumulated silk.

The general range of webbing behavior recorded for *Larinioides* is paralleled in *Tetragnatha*, although this much larger and ecologically more diverse genus collectively displays an even greater tendency to deviate from typical orb construction. The latter is usually diagonal or horizontal and relatively fragile, with some species remaining at the hub both day and night, and others mainly crepuscular (LeSar and Unzicker 1978, Levi 1981, Gillespie 1987a, Aiken and Coyle 2000, Dondale et al. 2003). However, at least one North American species (*T. viridis* Walckenaer) does not spin a web (Edwards and Edwards 1997, Aiken and Coyle 2000), while others readily aggregate and produce shared, non-orb silk in response to high prey density (Buskirk 1986, Gillespie 1987b).

T. guatemalensis ranges as far north as Nova Scotia, although many U.S. records are clustered in Florida and south Texas, and the species has been collected as far south as Panama (Levi 1981, Dondale et al. 2003). Unlike *L. sclopetarius*, it has largely escaped the attention of biologists, with one conspicuous exception. In 2007, a huge expanse of communal webbing, created mainly by *T. guatemalensis* (but also

containing at least five araneids, including a *Larinioides* sp.) was discovered at Lake Tawakoni State Park in Texas. Consisting of irregular masses of both sheet-like and volumetric silk for about 80–100 m along a woodland trail and enveloping several trees 10–20 m tall, the “giant Texas web” quickly became an international media and Internet sensation, in large part due to compelling photographs of what was presented as a rare, if not unique, phenomenon (Quinn 2007, Jackman et al. 2007, Guarisco 2008). Observations suggested that at least some, and perhaps the majority, of the sheet-like webbing was formed and enhanced by the cumulative drag lines of wandering males (which were also recorded by Uetz, 1986, on the huge Cincinnati *L. sclopetarius* web), whereas the irregular, three-dimensional silk might have been due in part to the repeated construction of typical tetragnathid retreat webbing (Lapp 2007a, b, c). In response to this event, photographs and descriptions of other uncommonly large, tetragnathid-dominated webs shrouding vegetation were posted on the Internet (Quinn 2007).

Although we have only a rudimentary understanding of the population dynamics and behavior of otherwise solitary orb-weaving spiders in megawebs, these spectacular events may therefore be less unique than is generally believed. Due to its location in a modular structure that allowed the extent of its webbing and size of its population to be more readily quantified than in most non-anthropogenic habitats, the Back River aggregation has furnished a detailed overview of what is by far the most extreme example of its genre. Combined with previously published accounts, the following generalizations can be made:

- 1) Spiders display broad and interrelated spectra of plasticity in web construction and degree of territoriality, with shared silk and tolerance for neighbors often increasing with high prey density. These behavioral precedents demonstrate that, despite their potential for attaining an awe-inspiring scale, megawebs differ from much smaller aggregations of solitary orb-weavers mainly by degree. The massive communal constructions are all the more impressive since individual web production decreases when orb-weavers are well fed.

- 2) At this point, all published examples of megawebs have been primarily produced by representatives of two genera – indeed, almost exclusively two species, *T. guatemalensis* and *L. sclopetarius* – that appear to have a strong tendency toward this behavior. Not surprisingly, the Lake Tawakoni webbing contained far more taxonomic diversity (at least 21 spider genera in 12 families as reported by Jackman et al. 2007) than was present at Back River (9 genera in 6 families) due to its location in a commensurately more complex outdoor habitat. However, whether present due to opportunistic or inadvertent reasons, it is clear that most of the taxa at both sites were relatively incidental to the total output of silk. Both the Texas and Maryland aggregations were similar in that *T. guatemalensis* was significantly more numerous than co-existing araneids. Such aggregations in temperate climates may be substantially larger in the fall, when *Tetragnatha* populations typically peak (Williams et al. 1995), although exposed webs are highly susceptible to damage from severe weather (Lapp 2007a,b).

- 3) All recorded megawebs have occurred in close proximity to a riparian habitat that provided a sustainable reservoir of prey. The vital link to an aquatic or marine food source has been a prominent focus in ecological studies of allochthonous nutrient transfer to adjacent terrestrial systems, with the beneficiaries of these resource “subsidies” including an enormous variety of plants and animals (Polis et al. 1997). In particular, adult chironomid midges and other emerging

aquatic insects have been shown to play a dominant role in supplying nutrition to orb-weaving spiders living on the margins of streams, rivers, and lakes (Baxter et al. 2005), including *L. scolopetarius* (Heiling and Herberstein 1998, Heiling 1999) and various *Tetragnatha* spp. (Williams et al. 1995; Henschel et al. 2001; Collier et al. 2002; Sanzone et al. 2003; Kato et al. 2003, 2004; Akamatsu 2004). Chironomids constituted the overwhelming majority of prey in the Back River web on our sampling date (Fig. 9) and were still heavily swarming around the facility in mid-December (see discussion below). Both chironomids and mosquitoes from the adjacent lake and wetlands appeared to be the principal prey for the Lake Tawakoni aggregation (Lapp 2007a,b; Jackman et al. 2007; Guarisco 2008).

4) Although individual orbs may persist in a megaweb matrix, the architecture is characterized by extensive laminar and volumetric webbing. Various behavioral mechanisms have been proposed to explain these two types of construction in dense orb-weaver aggregations, but there have been no detailed, long-term studies of their origin and maintenance. Inasmuch as typical orb webs are famous as solitary constructs that achieve their purpose with a minimum of time, energy, and material (Shear 1986, Foelix 1996), it is somewhat incongruous that species such as *L. scolopetarius* and *T. guatemalensis* are capable of collectively producing massive outputs of shared, three-dimensional silk that are the exact opposite of the spare, planar, radially-symmetric orbs these spiders create as individuals in most circumstances. Since taxa that characteristically construct complex, three-dimensional webs are a relatively recent phylogenetic development within the orbicularian Araneae (Coddington and Levi 1991, Griswold et al. 1998, Blackledge et al. 2003), the ability of more basal orb-weavers to organize silk in this manner is a testament to the behavioral flexibility that may well have expedited the progression of web evolution.

Spider Colonization and Hyperabundance In Structural Habitats. The prominence of spiders as predictable and persistent inhabitants of virtually every type of built environment is unmatched by any other group of predatory arthropods and is a recurring theme of urban entomology as an ecological discipline. A unique combination of behavioral and physiological attributes as well as the distinctive environmental conditions inherent to new, barren ecosystems are responsible for this success. Of major importance is that spiders as a group are exceptionally vagile, not just as pedestrians within a local area but also by the passive mechanisms of anthropochoric transport and ballooning that potentially result in rapid, long-range dispersal. Particularly the latter behavior enables them to reliably drift onto remote islands and the earliest successional substrates created by fire, volcanoes, retreating glaciers, and human activity (Meijer 1977, Schoener and Toft 1983, Crawford et al. 1995, Polis and Hurd 1995, Buddle et al. 2000, Hodkinson et al. 2001). Confronted by formidable challenges in these environments, they benefit from a low metabolic rate, conferring a resistance to starvation (Kotiaho 1998), and, in many cases, low predation pressure and competition for resources from the relatively few other taxa in these simple systems (Schoener and Toft 1983, Wise 1993, Polis and Hurd 1995). Buildings present circumstances similar to most other types of pioneer habitats for arthropod colonization, and can be expected to reflect the same fundamental principles of island biogeography and metapopulation dynamics as isolated habitat patches in non-anthropogenic environments (Hanski 1999, Whittaker and Fernández-Palacios 2007, Losos and Ricklefs 2010).

In fact, although species at higher trophic levels generally are

more vulnerable to extinction in insularized ecosystems (Holt et al. 1999), structures often represent immense reservoirs of protected living space for various spider species that are unmatched by any non-anthropogenic counterpart. Paralleling their wide range of sociality, spiders also display an equally broad spectrum of synanthropy, from occasional, facultative invaders of the built environment to near-obligate inhabitants that occur practically nowhere else, particularly in colder climates (Kaston 1983, Edwards and Edwards 1997, Guarisco 1999). At the extreme end of this spectrum are the few species that readily become hyperabundant when both sufficient refugia and a sustainable and abundant supply of either autochthonous or allochthonous prey are available. Recluse (*Loxosceles* spp.) and cellar spiders (Pholcidae, particularly *Pholcus phalangioides* Fuesslin) are often considered as models for achieving remarkably high densities within typical buildings, exploiting surroundings that mimic what is assumed to be their original claustral or cavernicolous habitats (Newlands 1981, Hopkin 1998, Vetter and Barger 2002, Greene et al. 2009).

However, there is another, quite different model for extreme spider success due to human construction. By far the largest spider aggregations in structural environments involve species not normally associated with secluded building interiors but able to colonize certain types of facilities that are relatively open to their surroundings and incorporate, or are in close proximity to, a source of aquatic prey that exceeds the ability of predators to deplete. The best documented example of this is a unique series of reports on the unparalleled density of linyphiid spiders (as high as 67,365 individuals per m³) in the stone medium of percolating filter beds at a sewage treatment works in Birmingham, UK (Duffey 1979, 1997; Duffey and Green 1975). The Linyphiidae is a wind-dispersed group of mostly tiny spiders known as sheet-web weavers that characteristically thrive in highly disturbed and exposed habitats, and have been shown to benefit from the increase in mesic conditions due to human activity in both agricultural and urban sites (Vanuytven 1986, Shochat et al. 2004). The Birmingham filter beds, which supported a variety of small invertebrate grazers (primarily enchytraeid worms and dipteran larvae) on the biofilm coating the stones, were characterized as “a ‘super habitat’ in which the life strategy requirements of the two dominant spider species are maximized and competition from other species is minimized” (Duffey 1997). Duffey and Green (1975) noted that the numbers of the most abundant of these linyphiids in its natural marshland communities “are never, even remotely, near those shown to occur in the extremely artificial environment of a sewage filter-bed.”

The Back River sand filtration facility joins this precedent of exceptional arachnid productivity in a wastewater treatment plant, albeit with two much larger orb-weaving species, both of which are riparian but markedly different in their affinity for anthropogenic habitats. *T. guatemalensis*, like many other members of its genus, is strongly associated with the margins of streams, rivers, and lakes, but not particularly in a structural context (Levi 1981, Dondale et al. 2003). In contrast, the holarctic *L. scolopetarius* is only rarely observed on vegetation, and is often termed the “bridge orb-weaver” because it so commonly occurs on these structures (and other human constructions near water) in both Europe and the U.S. (Wąsowska 1973, Levi 1974, Ware and Opell 1989, Heiling and Herberstein 1998, Heiling 1999, Howes 1999, Dondale et al. 2003). It has been suggested that this distinctive synanthropic preference may be due to the species’ original habitat of overhanging river banks that have since been

widely eliminated by human engineering (Howes 1999).

Wastewater treatment plants are one category of a wide array of aquacentric structures that range in size and complexity from modest bridges, docks, and boathouses to giant hydroelectric facilities, factories, and stadiums. Many of these buildings present buffered environments that are potentially “super habitats” for web-building spiders. In particular, the Back River facility offered two critical advantages over an outdoor site such as the Lake Tawakoni woodland trail. The first was shelter from inclement weather, which severely damaged the Texas web in August shortly after its discovery (Lapp 2007a,b) and undoubtedly acted as a check on its growth throughout the summer. Some *Tetragnatha* species are especially sensitive to rain, strong wind, and low temperatures, and will not construct webs in these conditions (LeSar and Unzicker 1978, Gillespie and Caraco 1987).

The building’s second critical asset was that it reliably and continually generated at least part of its spiders’ food supply. Enormous populations of chironomids living in the warm, nutrient-rich water of sewage treatment plants are well-documented (Gibson 1945, Armitage et al. 1995, Ali 1996), and sampling of the Back River filtration beds on 22 February 2010 confirmed that chironomid larvae were abundant in the sand. The water in the facility was about 10° C on that date, whereas ambient temperatures away from the building averaged about 4° C. Sparse numbers of adult midges flew over the filtration beds and water channels, whereas none were observed away from the building. Earlier in the winter, on 14 December 09, water temperature was about 15° C, ambient temperatures away from the building averaged about 10° C, and extremely dense clouds of swarming midges hovered along sections of the facility’s roofline.

Therefore, although chironomids that sustain populations of web-building spiders are almost always an allochthonous input (Hodkinson et al. 2001, Baxter et al. 2005), the Back River facility was at least partially self-contained, producing a renewable, autochthonous source of prey. The closed system dynamics clearly extended to many of the predators as well, since at least the *T. guatemalensis* population appeared to be overwhelmingly renewed from egg sacs deposited inside the building. In this regard, despite the considerable architectural differences, the sand filtration facility could nevertheless be considered as fundamentally similar to the subterranean urban infrastructure that harbors dense populations of *Loxosceles rufescens* (Dufour) sustained by autochthonous sources of cockroach and termite prey (Greene et al. 2009). Since much of the colonization of the facility was self-perpetuating and consisted of individuals living in the location for their entire life cycle, it is questionable whether the word “aggregation” (which often implies immigration to a site) is the most precise terminology for this instance.

It is noteworthy that the Back River plant managers emphasized that the facility’s immense spider concentration in 2009 differed from those in past years only by degree, and that its operations had never been significantly affected. Our recommendations for amelioration included the following general points:

- 1) On-site personnel should be reassured that the spiders are harmless and the facility’s immense shroud of silk should be presented in a positive light as a record-breaking natural history wonder.
- 2) Pesticides or chemical web-deterrent products, as suggested by local pest control companies, are unnecessary and inappropriate in light of the close proximity to treated water.
- 3) Web and spider removal is basically a recurring custodial func-

tion that should be accomplished by the most feasible mechanical means and on a schedule dependent on the buildup of new webbing.

- 4) Lighting of the facility is already minimal, and does not seem to be a critical factor in attracting additional spiders. However, more frequent rotational drying of the sand beds might be effective in lowering on-site midge populations.

The “Back River Arachnotopia” (as we referred to it in our educational material furnished to the plant managers) thus highlights the utility of aquacentric structures as accessible research sites where the dynamics of predictable spider hyperabundance can be closely examined under relatively comfortable conditions. In some respects—i.e. in its combination of reduced and indirect lighting, ideal web-attachment surfaces, benign and humid microclimate, and continuously renewable food reservoir—the sand filtration building is a gigantic replica of carefully designed orb-weaver culturing facilities such as the highly successful display of *Nephila inaurata* Thorell at the National Zoological Park in Washington, D.C. (Robinson and Miller 2007). As urban entomology matures as an ecologically-based discipline independent of economic considerations, this type of fortuitous, enhanced field plot will become increasingly important to its practitioners. 

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References Cited

- Aiken, M., and F. A. Coyle. 2000. Habitat distribution, life history and behavior of *Tetragnatha* spider species in the Great Smoky Mountains National Park. *J. Arachnol.* 28: 97-106.
- Akamatsu, F., H. Toda, and T. Okino. 2004. Food source of riparian spiders analyzed by using stable isotope ratios. *Ecol. Res.* 19: 655-662.
- Ali, A. 1996. A concise review of chironomid midges (Diptera: Chironomidae) as pests and their management. *J. Vector Ecol.* 21: 105-121.
- Armitage, P. D., P. S. Cranston, and L. C. V. Pinder (eds.). 1995. *The Chironomidae: the biology and ecology of non-biting midges.* Chapman & Hall, London, UK.
- Baxter, C. D., K. D. Fausch, and W. C. Saunders. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. *Freshwater Biol.* 50: 201-220.
- Blackledge, T. A., J. A. Coddington, and R. G. Gillespie. 2003. Are three-dimensional spider webs defensive adaptations? *Ecol. Lett.* 6: 13-18.
- Blackledge, T. A., and J. M. Zevenbergen. 2007. Condition-dependent spider web architecture in the western black widow, *Latrodectus hesperus*. *Anim. Behav.* 73: 855-864.
- Buddle, C. M., J. R. Spence, and D. W. Langor. 2000. Succession of boreal forest spider assemblages following wildfire and harvesting. *Ecography* 23: 424-436.
- Burgess, J. W., and G. W. Uetz. 1982. Social spacing strategies in spiders, pp. 317-351. In Witt, P. N., and J. S. Rovner (eds.), *Spider communication: mechanisms and ecological significance.* Princeton Univ. Press, Princeton, NJ.
- Buskirk, R. E. 1986. Orb-weaving spiders in aggregations modify individual web structure. *J. Arachnol.* 14: 259-265.
- Coddington, J. A., and H. W. Levi. 1991. Systematics and evolution of spiders (Araneae). *Ann. Rev. Ecol. Syst.* 22: 565-592.
- Collier, K. J., S. Bury, and M. Gibbs. 2002. A stable isotope study of linkages

- between stream and terrestrial food webs through spider predation. *Freshwater Biol.* 47: 1651-1659.
- Crawford, R. L., P. M. Sugg, and J. S. Edwards. 1995.** Spider arrival and primary establishment on terrain depopulated by volcanic eruption at Mount St. Helens, Washington. *Am. Midl. Nat.* 133: 60-75.
- Dondale, C. D., J. H. Redner, P. Paquin, and H. W. Levi. 2003.** The insects and arachnids of Canada. Part 23. The orb-weaving spiders of Canada and Alaska (Araneae: Uloboridae, Tetragnathidae, Araneidae, Theridiosomatidae). NRC Research Press, Ottawa, Ontario, Canada.
- Duffey, E. 1979.** Aerial dispersal by linyphiid spiders from filter beds on the Birmingham sewage works. *Newsl. Br. Arachnol. Soc.* 26: 3-4.
- Duffey, E. 1997.** Spider adaptation to artificial biotopes: the fauna of percolating filter beds in a sewage treatment works. *J. Appl. Ecol.* 34: 1190-1202.
- Duffey, E., and M. B. Green. 1975.** A linyphiid spider biting workers on a sewage-treatment plant. *Bull. Br. Arachnol. Soc.* 3: 130-131.
- Edwards, R. L., and E. H. Edwards. 1997.** Behavior and niche selection by mailbox spiders. *J. Arachnol.* 25: 20-30.
- Enders, F. 1974.** Vertical stratification in orb-web spiders (Araneidae, Araneae) and a consideration of other methods of coexistence. *Ecology* 55: 317-328.
- Foelix, R. F. 1996.** *Biology of spiders* (2nd edition). Oxford Univ. Press, Oxford, UK.
- Gibson, N. H. E. 1945.** On the mating swarms of certain Chironomidae (Diptera). *Trans. Roy. Entomol. Soc. London* 95: 263-294.
- Gillespie, R. G. 1987a.** The mechanism of habitat selection in the long-jawed orb-weaving spider *Tetragnatha elongata* (Araneae, Tetragnathidae). *J. Arachnol.* 15: 81-90.
- Gillespie, R. G. 1987b.** The role of prey availability in aggregative behaviour of the orb weaving spider *Tetragnatha elongata*. *Anim. Behav.* 35: 675-681.
- Gillespie, R. G., and T. Caraco. 1987.** Risk-sensitive foraging strategies of two spider populations. *Ecology* 68: 887-899.
- Greene, A., N. L. Breisch, T. Boardman, B. B. Pagac, E. Kunickis, R. K. Howes, and P. V. Brown. 2009.** The Mediterranean recluse spider, *Loxosceles rufescens* (Dufour): an abundant but cryptic inhabitant of deep infrastructure in the Washington, D.C. area (Arachnida: Araneae: Sicariidae). *Am. Entomol.* 55: 158-167.
- Griswold, C. E., J. A. Coddington, G. Hormiga, and N. Scharff. 1998.** Phylogeny of the orb-web building spiders (Araneae, Orbiculariae: Deinopoidea, Araneoidea). *Zool. J. Linn. Soc.* 123: 1-99.
- Guarisco, H. 1999.** House spiders of Kansas. *J. Arachnol.* 27: 217-221.
- Guarisco, H. 2008.** Silk city. *Nat. Hist.* 117(2): 80.
- Hanski, I. 1999.** *Metapopulation ecology*. Oxford Univ. Press, Oxford, UK.
- Heiling, A. M. 1999.** Why do nocturnal orb-web spiders (Araneidae) search for light? *Behav. Ecol. Sociobiol.* 46: 43-49.
- Heiling, A. M., and M. E. Herberstein. 1998.** The web of *Nuctenea sclopeteria* (Araneae, Araneidae): relationship between body size and web design. *J. Arachnol.* 26: 91-96.
- Heiling, A. M., and M. E. Herberstein. 2000.** Interpretations of orb-web variability: a review of past and current ideas. *Ekol. Bratislava* 19: 97-106.
- Henschel, J. R., D. Mahsberg, and H. Stumpf. 2001.** Allochthonous aquatic insects increase predation and decrease herbivory in river shore food webs. *Oikos* 93: 429-438.
- Herberstein, M. E., C. L. Craig, and M. A. Elgar. 2000.** Foraging strategies and feeding regimes: web and decoration investment in *Argiope keyserlingi* Karsch (Araneae: Araneidae). *Evol. Ecol. Res.* 2: 69-80.
- Hodkinson, I. D., S. J. Coulson, J. Harrison, and N. R. Webb. 2001.** What a wonderful web they weave: spiders, nutrient capture and early ecosystem development in the high Arctic – some counter-intuitive ideas on community assembly. *Oikos* 95: 349-352.
- Holt, R. D., J. H. Lawton, G. A. Polis, and N. D. Martinez. 1999.** Trophic rank and the species-area relationship. *Ecology* 80: 1495-1504.
- Hopkin, S. 1998.** The highest density of *Pholcus* in Britain? *Newsl. Br. Arachnol. Soc.* 83: 10
- Howes, C.A. 1999.** Spiders get new web site: *Larinioides sclopeteria* (Clerck, 1757) at Sykehouse Aqueduct, S. Yorkshire. *Newsl. Br. Arachnol. Soc.* 85: 6-7.
- Jackman, J. A., A. Dean, and M. Quinn. 2007.** Spiders from a large web at Lake Tawakoni, Texas. *Southwest. Entomol.* 32: 195-202.
- Kaston, B. J. 1983.** Synanthropic spiders, pp. 221-245. In Frankie, G. W., and C. S. Koehler (eds.), *Urban entomology: interdisciplinary perspectives*. Praeger, NY.
- Kato, C., T. Iwata, S. Nakano, and D. Kishi. 2003.** Dynamics of aquatic insect flux affects distribution of riparian web-building spiders. *Oikos* 103: 113-120.
- Kato, C., T. Iwata, and E. Wada. 2004.** Prey use by web-building spiders: stable isotope analyses of trophic flow at a forest-stream ecotone. *Ecol. Res.* 19: 633-643.
- Kotiaho, J. S. 1998.** Sexual differences in metabolic rates of spiders. *J. Arachnol.* 26: 401-404.
- Lapp, J. 2007a.** Tawakoni visit report. Univ. Houston, TX-ENTO Archives – Sept. 2007 (#2). (<http://listserv.uh.edu/cgi-bin/wa?A2=ind0709&L=tx-ento&T=0&P=149>)
- Lapp, J. 2007b.** Lake Tawakoni 9/19 trip report (long). Univ. Houston, TX-ENTO Archives – Sept. 2007 (#25). (<http://listserv.uh.edu/cgi-bin/wa?A2=ind0709&L=tx-ento&T=0&O=D&P=2650>)
- Lapp, J. 2007c.** Lake Tawakoni 9/19 trip report (long). Univ. Houston, TX-ENTO Archives – Sept. 2007 (#26). (<http://listserv.uh.edu/cgi-bin/wa?A2=ind0709&L=tx-ento&T=0&P=2757>)
- Leborgne, R., and A. Pasquet. 1987.** Influences of aggregative behaviour on space occupation in the spider *Zygiella x-notata* (Clerck). *Behav. Ecol. Sociobiol.* 20: 203-208.
- Leech, R. 2003.** Enormous concentration of the wheelhouse spider [*Nuctenea patagiata* (Clerck)] at the Lake Wabamun power plant wheelhouse (Araneae: Araneidae). *Can. Arachnol.* 4: 13-15.
- LeSar, C. D., and J. D. Unzicker. 1978.** Life history, habits, and prey preferences of *Tetragnatha laboriosa* (Araneae: Tetragnathidae). *Environ. Entomol.* 7: 879-884.
- Levi, H. W. 1974.** The orb-weaver genera *Araniella* and *Nuctenea* (Araneae: Araneidae). *Bull. Mus. Comp. Zool.* 146: 291-316.
- Levi, H. W. 1981.** The American orb-weaver genera *Dolichognatha* and *Tetragnatha* north of Mexico (Araneae: Araneidae, Tetragnathinae). *Bull. Mus. Comp. Zool.* 149: 271-318.
- Lloyd, N. J., and M. A. Elgar. 1997.** Costs and benefits of facultative aggregating behaviour in the orb-spinning spider *Gasteracantha minax* Thorell (Araneae: Araneidae). *Aust. J. Ecol.* 22: 256-261.
- Losos, J. B., and R. E. Ricklefs (eds.). 2010.** *The theory of island biogeography revisited*. Princeton Univ. Press, Princeton, NJ.
- Meijer, J. 1977.** The immigration of spiders (Araneida) into a new polder. *Ecol. Entomol.* 2: 81-90.
- Newlands, G. 1981.** A new violin spider from Johannesburg with notes on its medical and epidemiological importance. *Z. Angew. Zool.* 68: 357-365.
- Pasquet, A., A. Ridwan, and R. Leborgne. 1994.** Presence of potential prey affects web-building in an orb-weaving spider *Zygiella x-notata*. *Anim. Behav.* 47: 477-480.
- Polis, G. A., and S. D. Hurd. 1995.** Extraordinarily high spider densities on islands: flow of energy from the marine to terrestrial food webs and the absence of predation. *Proc. Natl. Acad. Sci.* 92: 4382-4386.
- Polis, G. A., W. B. Anderson, and R. D. Holt. 1997.** Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Ann. Rev. Ecol. Syst.* 28: 289-316.
- Quinn, M. 2007.** Giant spider web in an east Texas state park – 2007. (http://www.texasento.net/Social_Spider.htm)
- Robinson, B., and M. J. Miller. 2007.** *Nephila madagascarensis* (Vinson) (Araneae: Tetragnathidae) at the National Zoo. *Am. Arachnol.* 74: 9.
- Roush, R. S., and D. C. Radabaugh. 1993.** Web density is related to prey abundance in cellar spiders, *Pholcus phalangioides* (Fuesslin) (Araneae: Pholcidae). *Bull. Br. Arachnol. Soc.* 9: 142-144.
- Rypstra, A. L. 1985.** Aggregations of *Nephila clavipes* (L.) (Araneae, Araneidae) in relation to prey availability. *J. Arachnol.* 13: 71-78.
- Salomon, M. 2007.** Western black widow spiders express state-dependent web-building strategies tailored to the presence of neighbours. *Anim. Behav.* 73: 865-875.
- Sanzone, D. M., J. L. Meyer, E. Marti, E. P. Gardiner, J. L. Tank, and N. B. Grimm. 2003.** Carbon and nitrogen transfer from a desert stream to riparian predators. *Oecologia* 134: 238-250.
- Schoener, T. W., and C. A. Toft. 1983.** Spider populations: extraordinarily high densities on islands without top predators. *Science* 219: 1353-1355.

- Schuck-Paim, C., and W. J. Alonso. 2001.** Deciding where to settle: conspecific attraction and web site selection in the orb-web spider *Nephilengys cruentata*. *Anim. Behav.* 62: 1007-1012.
- Segoli, M., A. Maklakov, E. Gavish, I. Tsurim, and Y. Lubin. 2004.** The effect of previous foraging success on web-building behaviour in the sheet-web spider *Frontinellina cf. frutetorum* (Araneae: Linyphiidae). *Ethol. Ecol. Evol.* 16: 291-298.
- Shear, W. A. 1986.** The evolution of web-building behavior in spiders: a third generation of hypotheses, pp. 364-400. In Shear, W. A. (ed.), *Spiders: webs, behavior, and evolution*. Stanford Univ. Press, Stanford, CA.
- Sherman, P. M. 1994.** The orb-web: an energetic and behavioural estimator of a spider's dynamic foraging and reproductive strategies. *Anim. Behav.* 48: 19-34.
- Shochat, E., W. L. Stefanov, M. E. A. Whitehouse, and S. H. Faeth. 2004.** Urbanization and spider diversity: influences of human modification of habitat structure and productivity. *Ecol. Appl.* 14: 268-280.
- Thévenard, L., R. Leborgne, and A. Pasquet. 2004.** Web-building management in an orb-weaving spider, *Zygiella x-notata*: influence of prey and conspecifics. *C. R. Biol.* 327: 84-92.
- Tso, I-M. 1999.** Behavioral response of *Argiope trifasciata* to recent foraging gain: a manipulative study. *Am. Midl. Nat.* 141: 238-246.
- Uetz, G. W. 1986.** Web building and prey capture in communal orb weavers, pp. 207-231. In Shear, W. A. (ed.), *Spiders: webs, behavior, and evolution*. Stanford Univ. Press, Stanford, CA.
- Uetz, G. W., and C. S. Hieber. 1997.** Colonial web-building spiders: balancing the costs and benefits of group-living, pp. 458-475. In Choe, J. C., and B. J. Crespi (eds.), *Social behavior in insects and arachnids*. Cambridge Univ. Press, Cambridge, UK.
- Vanuytven, H. 1986.** The spiderfauna of the Antwerp sewers (Araneae). *Phegea* 14: 127-129.
- Vetter, R. S., and D. K. Barger. 2002.** An infestation of 2,055 brown recluse spiders (Araneae: Sicariidae) and no envenomations in a Kansas home: implications for bite diagnoses in nonendemic areas. *J. Med. Entomol.* 39: 948-951.
- Ware, A. D., and B. D. Opell. 1989.** A test of the mechanical isolation hypothesis in two similar spider species. *J. Arachnol.* 17: 149-162.
- Wąsowska, S. 1973.** The variability of the number of external spinning structures within one population of *Araneus sclopetarius* Clerck. *Zool. Poloniae* 23: 109-118.
- Whitehouse, M. E. A., and Y. Lubin. 2005.** The functions of societies and the evolution of group living: spider societies as a test case. *Biol. Rev.* 80: 347-361.
- Whittaker, R. J., and J. M. Fernández-Palacios. 2007.** *Island biogeography: ecology, evolution, and conservation*. Second ed. Oxford Univ. Press, Oxford, UK.
- Williams, D. D., L. G. Ambrose, and L. N. Browning. 1995.** Trophic dynamics of two sympatric species of riparian spider (Araneae: Tetragnathidae). *Can. J. Zool.* 73: 1545-1553.
- Wise, D. H. 1993.** *Spiders in ecological webs*. Cambridge Univ. Press, Cambridge, UK.
- Wise, D. H. 2006.** Cannibalism, food limitation, intraspecific competition, and the regulation of spider populations. *Ann. Rev. Entomol.* 51: 441-465.
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