Harvestmen (Opiliones) of the Savannah River Site, South Carolina

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Abstract - A year-long continuous pitfall trapping program in 8 habitats at the Savannah River Site on South Carolina's coastal plain yielded over 4200 individual Opiliones, and the resulting data set provides a fine-grained description of Opiliones faunistics, habitat distribution, and phenology in southeastern North America, where Opiliones biology has been neglected. The 9 species reported from the site include a new state record (*Vonones sayi*), a rarely reported species (*Bishopella laciniosa*), and a common species that was undescribed at the time of the study (*Hadrobunus fusiformis*). All species abundant enough to examine seem to be univoltine and to reproduce in the warm season (adults mostly present in autumn), but species varied greatly in seasonality and duration of the peak adult sample period and in their habitat distribution. *Leiobunum bimaculatum* preferred xeric sites, *H. fusiformis* was widely distributed across habitats, and the other species were generally more abundant in more mesic habitats. Richness estimation showed that the ground-accessible Opiliones fauna was adequately sampled by this pitfall regime.

Introduction

The harvestmen (Order Opiliones) are the third-most diverse group of arachnids after spiders and mites. More than 6000 species have been described, and it is estimated that there are 10,000 species worldwide (Pinto-da-Rocha et al. 2007). Over 200 species are known from North America (Cokendolpher and Lee 1993), and they are diverse and ecologically important predator/scavengers in the southeastern United States. Prior to this investigation, 19 harvestman species were known from South Carolina, including 3 undescribed *Hadrobunus* species (Table 1). Although this number is fairly typical for a southern state (Cokendolpher and Lee [1993] list 20 species from Georgia, 22 species from North Carolina, and 19 species from Tennessee), it is undoubtedly an underestimate because many of South Carolina's diverse ecosystems remain unsampled (Fig. 1) and the collecting that has occurred has been largely incidental. It is very likely that elements of the harvestman fauna of the southern Appalachians—such as *Leiobunum calcar* (Wood), *L. aldrichi* (Weed), *Odiellus pictus* (Wood), and *Caddo agilis* Banks—extend into the far northern portions of the state. Even *Phalangium opilio* L., a seemingly ubiquitous introduced species, has yet to be formally recorded. Unfortunately, the neglected status of harvestmen in South Carolina is also typical of most other states. Our study is one of the first to take a comprehensive approach to harvestmen diversity in the region.

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An intensive study of sheetweb-weaving spiders (Linyphiidae) on the Department of Energy's Savannah River Site (SRS) in South Carolina (Draney 1997) yielded many samples of Opiliones, giving us an opportunity to examine the fauna of a western region of this neglected state. Knowledge of the Opiliones fauna of this site is particularly important because the ecosystems of the SRS are among the most-intensively studied in southeastern North America. The site was established in 1951 for the production of weapons-grade nuclear materials, and although there has been considerable research into the effects of radiation on ecological processes, the site has also been managed as a de facto nature preserve since that time, and includes large tracts of some of the least-disturbed ecosystems on the southeastern coastal plain. The Savannah River Ecology Lab has published over 3300 articles since 1955 (http://srel.uga.edu/Reprint/REPRINTS.pdf). Consequently, this initial study of the harvestmen of SRS may be important in understanding Opiliones

Table 1. County-level list of Opiliones of South Carolina. See Table 2 for further information about taxa recorded in the present study.

Species	County (source)
Bishopella laciniosa (Crosby and Bishop)	Locality unspecified (Holsinger and Peck 1971); Aiken (present study)
Crosbycus dasycnemus (Crosby)	Oconee (Shear 1986)
Eumesosoma nigrum (Say)	Colleton, Florence, Jasper (Cokendolpher 1980)
Hadrobunus fusiformis Shultz	Aiken, Beaufort, Colleton (Shultz 2010); Aiken, Allendale, Barnwell (present study)
Hadrobunus grandis (Say)	Colleton (Shultz 2012)
Hadrobunus n. sp. 1	Berkeley, Charleston (J.W. Shultz, unpubl. data)
Hadrobunus n. sp. 2	Darlington (J.W. Shultz, unpubl. data)
Hadrobunus n. sp. 3	Horry (J.W. Shultz, unpubl. data)
Leiobunum bimaculatum Banks	Jasper (Davis 1934); Aiken, Barnwell (present study)
Leiobunum euserratipalpe Ingianni, McGhee, & Shultz	Greenwood (Bishop 1949)
Leiobunum nigropalpi (Wood)	Oconee (Ingianni et al. 2011)
Leiobunum politum Weed	Beaufort, Berkeley, Colleton, Florence, Greenwood, Kershaw (Davis 1934)
Leiobunum uxorium Crosby and Bishop	Beaufort, Berkeley (Davis 1934); Horry (McGhee 1970 as *L. speciosum*; Aiken (present study)
Leiobunum ventricosum (Wood)	Anderson (Gorsuch et al. 1989); Allendale (present study)
Leiobunum verrucosum (Wood)	Berkeley, Darlington (Davis 1934); Aiken, Allendale, Barnwell (present study)
Leiobunum vittatum (Say)	Beaufort, Greenwood (Davis 1934); Aiken, Allendale (present study)
Metasiro sassafrasensis Clouse and Wheeler	Pickens (Clouse and Wheeler 2014)
Metasiro savannahensis Clouse and Wheeler	Jasper (Clouse and Wheeler 2014)
Sabacon cavicolens (Packard)	Greenville (Hoffman 1955)
Vonones sayi (Simon)	Aiken, Allendale, Barnwell (present study)

ecology since the ecological context of these sites is very well known. The objectives of this work were to present the first survey of harvestmen occurring on the SRS, to describe and compare the ground-active Opiliones fauna from major habitat types at the SRS, and to summarize the basic habitat associations and phenological patterns of these species.

Methods

Sampling for harvestmen was done by the first author in the context of 2 studies of spiders (Araneae). Eight habitats were sampled using 2 standard methods:

Pitfall trapping – Ten 8.5-cm-diameter pitfall traps, containing 4% formalin (with a trace of detergent), each covered by a 39 cm x 19 cm x 9 cm cinder block rain roof suspended by propping a 7-cm brick at 1 end, were randomly placed (at 10 of 100 possible locations on a grid, each point 5 m apart) within a 0.25-ha (50 m x 50 m) plot, and operated continuously for 1 year (366 days; 1–4 May 1995 through 1–4 May 1996) in each of the 8 habitats. Contents were emptied in 2-week intervals. Total trapping effort was almost 80 trap-years (8 habitats x 10 traps x 1 year; a few traps were lost due to flooding or animal disturbance), which yielded 14,934 spiders (Draney 1997) and 4288 harvestmen.

Litter sampling – Litter samples were collected 6 times (24–28 April, 26–30 June, 1–5 September, and 13–20 November 1995; 27–28 January and 10–14 April

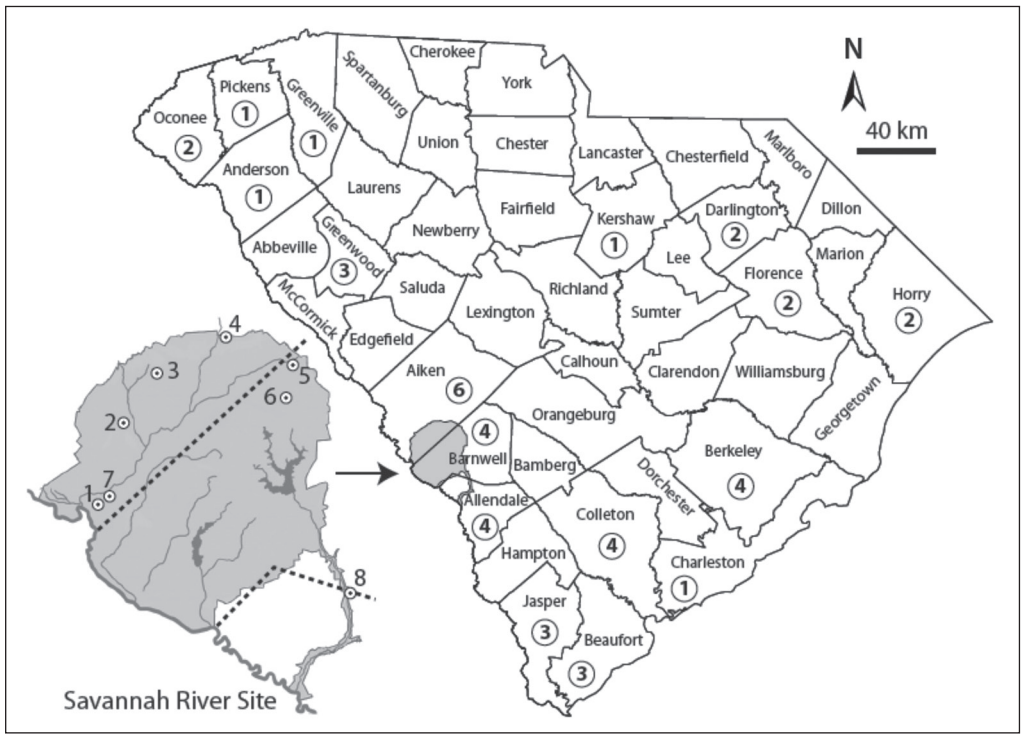

Figure 1. Map of South Carolina showing location of the Savannah River Site and 1995–1996 sampling sites 1–8. Numbers in circles are harvestmen species known per county; most counties are unsampled. For harvestman records by county, see Table 1.

1996). At each 0.25-ha site, two 0.04-m^2 litter samples were collected from each of 5 (of 100) randomly selected 5 m x 5 m subplots by driving a metal cylinder into the soil and collecting all leaf litter and debris down to mineral soil and hand sorting and sieving in the laboratory. Total sample effort was 19.2 m^2 (0.04 m^2 samples x 10 replicates x 6 dates x 8 habitats), which yielded 1178 spiders (Draney 1997) but only 11 harvestmen. See Draney (1997) and Draney and Crossley (1999) for additional site and sampling details.

Weather and climate

The average daily high and low temperatures during the study's trap year (May 1995–April 1996) were similar to the averages of the 30-year (1961–1990) climatic normal defined by the World Meteorological Organization (2016), at 24.78 °C and 9.94 °C versus 24.61 ± 0.77 °C (among-year standard deviation) and 11.0 ± 0.64 °C. Average low temperatures during the trap year were slightly lower than average, being more than 2.78 °C cooler than average in November and December 1995 and March 1996. Trap-year precipitation was significantly higher than the 30-year climatic normal mean (143.51 cm versus 119.38 ± 20.83 cm). The trap year saw higher precipitation than 28 of the 30 years in the 3-decade comparison period (National Weather Service data for Blackville, Barnwell County, SC, ~20 km east of SRS). In particular, June 1995 received 14.66 cm more than average, and August 1995 received 18.47 cm more than average.

Sites

These sites are listed here in order from the "youngest" habitats (most recently disturbed) to the "oldest" habitats (those with longest time since catastrophic disturbance such as fire or clearcutting). Sites 1–4 form an old field to pine forest successional sequence; sites 5, 6, and 7 represent typical xeric, mesic, and wet mesic subclimax forest types, respectively; and site 8 represents a mesic climax forest type. The majority of the study sites were on "set-aside areas", part of the DOE's research set-aside program. More information on those sites is available at http://srel.uga.edu/set-asides/set-asides.html.

1. Old field site: Savannah River Ecology Laboratory (SREL) Set-Aside No. 1 (Field 3-412), in Aiken County (33°13'30"N, 81°45'15"W), includes several hectares of forb–grassland. Maintenance as a pipeline right-of-way by annual mowing and herbicide applications keeps this habitat in an early successional stage, with no trees or shrubs. Site vegetation is dominated by perennial grasses interspersed with extensive mats of lichen (*Cladonia* spp.). *Opuntia humifusa* Rafinesque (Prickly Pear Cactus) is also abundant. Although this site receives the same amount of rain as the other sites, the excessively drained sandy soils, lack of tree cover, and very thin litter layer result in very xeric conditions for much of the year.

2. Young pines site: A 5-year-old (in 1996) plantation stand of *Pinus palustris* Miller (Longleaf Pine), located on 10 ha near the junction of SRS Road 2 and the M-Line Railroad in Aiken County (33°18'30"N, 81°43'30"W) represents young pine stands, which are biotically and abiotically intermediate between typical field and forest habitats in this region. The leaf-litter layer is thin in this transitional

habitat, barely covering the well-drained sandy soil, and resulting in a fairly xeric ground-layer environment for much of the year.

3. Medium pines site: SREL Set-Aside No. 2 in Aiken County (33°21'30"N, 81°41'W) includes about 27 ha of a 27-year-old (in 1996) plantation stand of Longleaf Pine. This site represents a "medium aged" pine habitat, successionally intermediate between the young and the mature pine stands. The ~15-m-tall pines supported a very thick litter layer (November litter depth mean ± std. dev. = 7.60 ± 3.28 cm) on sandy, well-drained soil.

4. Large pines site: SREL Set-Aside No. 4 is an 8.9-ha volunteer *Pinus taeda* L. (Loblolly Pine) stand in Aiken County (33°24'N, 81°36'W). It was ~40 years old in 1996 and is the result of natural succession of an agricultural field abandoned in 1951. The overstory is composed entirely of ~25-m-high Loblolly Pines, and there is only a sparse, low understory of *Quercus* spp. (oaks) and pine saplings. Groundcover is sparse and consists mainly of perennial grasses, *Toxicodendron radicans* (L.) Kuntze (Poison Ivy), and *Cladonia* sp. (reindeer moss lichen). The pine litter is thick, and woody debris accumulation is heavy. The soil is well drained and sandy.

5. Sandhill scrub oak/pine site: SREL Set-Aside No. 29 is a mature stand of oak and pine on a sandhill in Barnwell County (33°22'N, 81°31'W), which consists of a widely spaced canopy of ~10–20-m-tall Loblolly and Longleaf Pines and a thicker understory of ~3–10-m-tall oaks, mainly *Quercus laevis* Walter (Turkey Oak) and *Q. stellata* Wanghen (Post Oak). The herb layer is very sparse, consisting mostly of grasses. The site was in forest when the SRS was established in 1951; the oldest trees were about 81 years old in 1996. The excessively well-drained sandy soils on the 5–10% slope of the south-facing hillside result in xeric ground-layer conditions.

6. Upland hardwood site: This site, located in SRS Timber Compartment 30 off SRS Road 8-4 in Barnwell County (33°20'N, 81°31'30"W), is a mature oak–hickory stand consisting of moderate-sized oaks, especially *Quercus falcata* Michaux (Southern Red Oak) and *Q. marilandica* Muenchh. (Blackjack Oak), and *Carya tomentosa* Sarge (Mockernut Hickory). This forest was intact when the SRS was established in 1951, and is probably a relict or regrowth forest which regenerated after selective logging some time before 1951. The ground layer was dominated by grasses, Poison Ivy, and *Smilax* spp. (catbriers), and the soil is a loamy sand.

7. Riparian hardwood site: SREL Set-Aside No. 6 is a mature bottomland hardwood stand on the floodplain of Upper Three Runs Creek in Aiken County (33°14'N, 81°44'30"W). Most of the sampled area occurs on the low floodplain immediately adjacent to the river. This site was selectively logged in the 1920s and 1930s, but has not been cut or burned since. Portions of the floodplain are shallowly submerged during the winter. The canopy included *Quercus nigra* L. (Water Oak), Loblolly Pine, *Liquidambar styraciflua* L. (Sweetgum), and *Fagus grandifolia* Ehrh. (American Beech), with a diverse and often lush understory and ground layer. Soils consist of a silty clay flood deposit overlaying a thick sandy layer.

8. Riparian old-growth site: SREL Set-Aside No. 18 is an old-growth riparian forest on a terrace just above the floodplain of Lower Three Runs Creek in

Allendale County (33°08'N, 81°26'30"W). This 3.4-ha site includes the oldest canopy elements found at SRS: Loblolly Pines aged at 196–216 years in 1996. The canopy also comprised Sweetgum and *Liriodendron tulipifera* L. (Yellow Poplar). A dense under-canopy was dominated by Mockernut Hickory and oaks. The shrub layer and cover is sparse. Soils are well-drained and loamy; the litter layer includes a well-developed, root-bound humus layer.

Baseline survey

A baseline biodiversity survey was undertaken during the summer of 1992, prior to the previously described sampling. In each of the following 6 habitats, 20 two-day (~48-hour) uncovered ethanol pitfalls were run 7 times (27–29 November 1991; 27–28 April;,11–13 May, 16–18 June, 30 June–2 July;,15–17 July, and 2–4 October 1992). These traps were run in 4 lines of 5 traps with 3 m between traps. Harvestmen were collected by hand and using a sweep net during some of these dates as well. The sampling intensity was much less than for the 1995 project, yielding only 73 Opiliones specimens (66 from the pitfall trapping and 7 from sweep netting or hand collection). Therefore, these specimens serve to document additional records, but analysis of data is restricted to the 1995–1996 pitfall data. For more information about these sites, see Workman and McLeod (1990) and Davis and Janacek (1997).

1. Rainbow Bay (Set-Aside 16 in Barnwell County; 33°15.6'N, 81°37.9'W) is one of about 194 Carolina Bays on the SRS (Workman and McLeod 1990). These are shallow elliptical or ovoid ephemeral (winter-filled) wetlands. Rainbow Bay is about 1 ha in size.

2. A plantation of *Pinus elliotti* Engelm (Slash Pine) dominated woods surrounding Rainbow Bay (Set-Aside 16). Sampling took place outside of the wetland and within 100 m of it.

3. Powerline cut just northwest of Set-Aside 16 at the junction of Road C-5 and Road C-5e.3 (Barnwell County; 33°15'43"N, 81°38'4"W), dominated by a thick bramble cover of *Rubus* spp. (Blackberry) with some *Prunus serotina* Ehrh. (Black Cherry) growing as an overstory.

4. Sandhills xeric pine–oak forest set-aside (Set-Aside 3 in Aiken County; 33°16'57"N, 81°41'9"W) is a relatively undisturbed xeric forest dominated by Turkey Oak and Longleaf Pine on infertile, very well-drained sandy soil, which is a remnant ancient beach dune.

5. Beach hardwood riparian woods set-aside (same as site number 7, above).

6. Mixed riparian swamp set-aside (Set-Aside 7 in Barnwell County; 33°9'42"N, 81°43'35"W). This is a seasonally flooded bottomland hardwood forest on the floodplain of the Savannah River.

Data analysis

All harvestmen were identified by the second author, and vouchers are retained in the collections of both authors.

We restricted analyses to the 1 year of continuous pitfall trapping in 8 habitats during 1995–1996. This robust data set features virtually equal sampling effort among 8 major SRS habitat types and among 26 sampling dates of a continuously

sampled year (May 1995–May 1996). Therefore, it is possible to compare species richness, phenology, and habitat distribution among these 8 habitats.

Species richness. We used Estimate S (Colwell 2013) tto estimate the richness of the ground-dwelling Opiliones fauna at all 8 SRS study sites, both combined and separately, given the results of the pitfall sampling. The indices use the ratio of singletons (species represented by only one individual) to doubletons (species represented by exactly two individuals) in a sample and, with the assumption that there will be no singletons in a totally sampled assemblage, serve to reflect the number of unsampled taxa remaining. Thus, estimates could not be obtained from habitats lacking singletons and doubletons, but we pooled all adult individuals trapped during a year and analyzed the data as a single sample. We calculated an abundance-based species richness estimator called Chao 1 (Chao 1987).

We also used Estimate S to determine the similarity of the Opiliones assemblages in the pitfall samples among all pairs of the eight 1995–1996 habitats. We used Estimate S (Colwell 2013) to calculate the abundance-based Jaccard sample similarity index (Chao et al. 2005). The index ranges from 0 (no species shared between 2 habitats) to 1 (identical species composition and abundance).

Phenology. For the 5 species represented in the 1995–1996 pitfall data by more individuals than sample dates ($n > 26$), we calculated an index of seasonality (I_s; Curtis 1978), which uses the proportion of individuals of a species captured in each month to determine how evenly the species is distributed throughout the year. Since our sampling periods were biweekly instead of monthly, the index was converted to a fraction (proportion of the year) and then multiplied by 12 to express the index as "months", with smaller numbers denoting more stenochronous species (found as adults during only a short time each year), and larger numbers denoting relatively eurychronous species that are more widely distributed seasonally. The index varies from a minimum of 12/s to a maximum of 12 and is calculated as

$$I_s = 12[(1/\sum p_j^2)/s], \text{ summed over all sampling periods,}$$

where p_j = proportion sampled during sampling period j, and s = total number of sampling periods

Results

Species richness

Altogether, we sampled and examined 4372 Opiliones specimens: 4288 (98.1%) from the 1995–1996 pitfalls; 66 (1.51%) from the 1992 pitfalls; 11 (0.25%) from the 1995–1996 litter samples, and 7 (0.16%) from 1992 sweep-net and hand-collected samples. We found 9 species of harvestmen (Table 2). Table 1 and Figure 1 show the county-level records of Opiliones in South Carolina. One of the counties sampled here, Aiken, now has the most species reported from any county in the state, with 6. *Vonones sayi* is reported from South Carolina for the first time here, although it seems to occur at almost every South Carolina site we have collected, from the mountains to the coast, and it may well be present in every county in the state (M.L. Draney, pers. observ.). *Bishopella laciniosa* (Crosby and Bishop) (Phalangodidae), a species rarely collected in South Carolina and known from only 2 previous reports

Table 2. List of Opiliones from the Savannah River site, SC. See text for further information about sites and sampling methods. 1992 Sites: 1 = Rainbow Bay (Barnwell County); 2 = slash pine surrounding Rainbow Bay (Barnwell County); 3 = powerline cut brambles (Barnwell County); 4 = sandhills (Aiken County); 5 = beech hardwood (Aiken County); 6 = mixed swamp (Barnwell County). 1995 Sites (1992 site 5 = 1995 site 7): 1 = old field (Aiken County); 2 = young pine plantation (Aiken County); 3 = medium pines (Aiken County); 4 = large loblolly pines (Aiken County); 5 = sandhill scrub oak–pine (Barnwell County); 6 = upland hardwood (Barnwell County); 7 = beech hardwood (Aiken County); 8 = riparian old growth (Allendale County). See Figure 1. Counties: AK = Aiken, AD = Allendale, BW = Barnwell. Methods: P = Pitfall trap, L = Litter sorting, H = Hand collected.

Major Clade: Family	Species	1992 Sites	1995 Sites	Counties	Methods
Laniatores: Cosmetidae	*Vonones sayi* (Simon)	1, 2, 5, 6	4, 6, 7, 8	AK, AD, BW	P, L
Laniatores: Phalangodidae	*Bishopella laciniosa* (Crosby and Bishop)		7	AK	L
Palpatores: Sclerosomatidae	*Hadrobunus fusiformis* Shultz	1, 3, 4, 6	1, 2, 3, 4, 5, 6, 7, 8	AK, AD, BW	P,L
Palpatores: Sclerosomatidae	*Leobunum bimaculatum* Banks	1, 2	1, 2, 3, 4, 5	AK, BW	P, H
Palpatores: Sclerosomatidae	*Leiobunum politum* Weed	1	7, 8	AK, AD, BW	P
Palpatores: Sclerosomatidae	*Leiobunum uxorium* Crosby and Bishop		4, 7	AK	P
Palpatores: Sclerosomatidae	*Leiobunum ventricosum* (Wood)		8	AD	P
Palpatores: Sclerosomatidae	*Leiobunum verrucosum* (Wood)	5, 6	6, 7, 8	AK, AD, BW	P
Palpatores: Sclerosomatidae	*Leiobunum vittatum* (Say)		7, 8	AK, AD	P

(Fig. 1, Table 1), was the only species of the 9 not represented in the 1995–1996 pitfall samples; a single individual was collected from a litter sample at the Beech Hardwood Set-Aside #6, 1–5 September 1995. The Chao1 richness estimator could not be calculated on most of the assemblages from individual habitats, because of lack of singletons and doubletons in the data set. However, when all 1995–1996 pitfall data were pooled, the Chao1 richness estimate was the observed richness of 8 species.

Species composition

The 1995–1996 pitfall samples yielded 1 to 6 species per habitat (median = 3; Mean = 3.25; Table 3). In general, older and more-mesic habitats yielded more species than younger and more-xeric habitats (Table 3). The riparian hardwoods and riparian old-growth habitats each yielded 6 species, and the old field, young pines, and medium pines habitats each yielded only 2: *Leiobunum bimaculatum* Banks and *Hadrobunus fusiformis* Shultz. Only *L. bimaculatum* was collected in the xeric sandhill scrub oak–pine site. *Hadrobunus fusiformis* was numerically dominant overall in all habitats except the most xeric site, the old field (dominated by *L. bimaculatum*), and the most mesic site, the riparian hardwoods (dominated by *Leiobunum verrucosum* (Wood)). Diversity indices were not calculated to compare habitats because of very different sample sizes among them (n = 5 in sandhill oak–pine to n = 300 in riparian old growth) and because data were pooled over the course of a year. However, it is apparent that the more-mesic habitats have more-diverse assemblages of ground-active Opiliones, and that the species found at the riparian hardwoods site (Table 3) are remarkably evenly distributed and thus a highly diverse assemblage relative to the other sites.

Similarity among habitats

We used the classic Jaccard index to measure quantitative similarity of species composition (taking abundance into account) among all pairs of the 8 habitats

Table 3. Habitat distribution of pitfall-trapped Opiliones at the Savannah River Site, SC. Data given as percent of total adults trapped in 26 biweekly samples from May 1995 to May 1996 (pooled). See Methods for details about habitats. Habitats: 1 = old field, 2 = young pines, 3 = medium pines, 4 = large pines, 5 = sandhill oak–pine, 6 = upland hardwoods, 7 = riparian hardwoods, 8 = riparian old growth.

	Habitats								Total adults	No. of habitats
Species	1	2	3	4	5	6	7	8	trapped	occupied
Hadrobunus fusiformis	3.5	10.8	13.0	6.8	0.0	15.1	6.8	44.2	548	7
Leiobunum bimaculatum	51.2	31.7	3.7	7.3	6.1	0.0	0.0	0.0	82	5
L. politum	0.0	0.0	0.0	0.0	0.0	0.0	66.7	33.3	15	2
L. uxorium	0.0	0.0	0.0	75.0	0.0	0.0	25.0	0.0	4	2
L. ventricosum	0.0	0.0	0.0	0.0	0.0	0.0	0.0	100.0	4	1
L. verrucosum	0.0	0.0	0.0	0.0	0.0	4.8	70.5	24.8	105	3
L. vittatum	0.0	0.0	0.0	0.0	0.0	0.0	56.7	43.3	30	2
Vonones sayi	0.0	0.0	0.0	7.5	0.0	2.5	65.0	25.0	40	4
Habitat Richness	2	2	2	4	1	3	6	6		

sampled by pitfall in 1995–1996 (Table 4). Habitats shared 0–5 species (mean = 1.54, median and mode = 1). The similarity values ranged from 0 to 1, the theoretical minimum and maximum. The sandhill scrub oak–pine site (#5; see Table 3 for site abbreviations) shared no species with upland hardwoods (#6), riparian hardwoods (#7), and riparian old growth (#8). The old field (#1), young pines (#2) and medium pines (#3) habitats all shared the same 2 species: *Hadrobunus fusiformis* and *Leiobunum bimaculatum*. Average similarity across all habitat pairs was 0.38, and the median was 0.325. In general, the Jaccard similarity reflected the habitat's time since disturbance. The younger, more-xeric habitats had similar assemblages: pairs of habitats "1" through "5" always had values of 0.5 or 1.0, with the exception of 1 pair, the large pines and sandhills oak–pine. Likewise, habitats "6" through "8" always had values of 0.5 or higher (Table 4).

Habitat distribution of species

The 8 pitfall-sampled species were each recorded from 1 to 7 habitats (median = 2.5, mean = 3.25; Table 3). *Hadrobunus fusiformis* seems to be a habitat generalist,

Table 4. Species richness (Estimate S) of each habitat, and Jaccard Similarity between pairs of habitats for adult Opiliones at the Savannah River Site. Catch from the entire year's pitfalls was pooled. Habitats: 1 = old field, 2 = young pines, 3 = medium pines, 4 = large pines, 5 = sandhill oak–pine, 6 = upland hardwoods, 7 = riparian hardwoods, 8 = riparian old growth.

First habitat	Second habitat	S first habitat	S second habitat	Shared species	Jaccard similarity
1	2	2	2	2	1.000
1	3	2	2	2	1.000
1	4	2	4	2	0.500
1	5	2	1	1	0.500
1	6	2	3	1	0.250
1	7	2	6	1	0.143
1	8	2	6	1	0.143
2	3	2	2	2	1.000
2	4	2	4	2	0.500
2	5	2	1	1	0.500
2	6	2	3	1	0.250
2	7	2	6	1	0.143
2	8	2	6	1	0.143
3	4	2	4	2	0.500
3	5	2	1	1	0.500
3	6	2	3	1	0.250
3	7	2	6	1	0.143
3	8	2	6	1	0.143
4	5	4	1	1	0.250
4	6	4	3	2	0.400
4	7	4	6	3	0.429
4	8	4	6	2	0.250
5	6	1	3	0	0.000
5	7	1	6	0	0.000
5	8	1	6	0	0.000
6	7	3	6	3	0.500
6	8	3	6	3	0.500
7	8	6	6	5	0.714

being present in all habitats except the sandhill scrub oak–pine site (although an individual was collected from a similar xeric forested site, the sandhill set-aside # 3 in October 1992; Table 2). The species was common in both the wettest (riparian hardwoods) and driest (old field) sites, and across the range of disturbance frequency, from the frequently disturbed old field to the 200-year-old riparian old-growth site. It seems to be the most generalist in its habitat distribution, although 44.2% of the individuals were trapped in the riparian old-growth habitat.

Leiobunum bimaculatum seems to be distributed in more-xeric and more-frequently disturbed sites (Table 3). It was most abundant (51.1% of specimens) at the old field site and was absent from the older sites except for the xeric sandhill oak–pine site. It was the only species found in this xeric site.

The remaining 6 species all seem to be distributed mainly in the more-mesic and less-frequently disturbed sites. All 6 were absent from the 3 most-xeric and youngest sites (old field, young pines, and medium pines sites), and from the sandhill oak–pine site.

Phenology

Overall, adult Opiliones made up 23.5% of total individuals trapped in the 1995–1996 pitfalls. However, this ratio varied widely throughout the year (Table 5); the pitfall traps sampled between 0 and 5 species of adult harvestmen at any time period; 4 to 5 species were present continuously between late June and early December (Table 5). There were no immatures trapped during 26 June through 6 September, and there were only 3 adults trapped during 29 December through 3 May. Immatures (of all species; these were not further identified) made their appearance in pitfalls in September and peaked during late February/early March (Table 5). Five species are abundant enough (Table 5) to describe their seasonal distribution in the samples. *Vonones sayi* peaked earliest, in late May/early June, but adults were found during a long time period, from late February through early October. The other 4 species had adult peaks in the autumn, with *Leiobunum verrucosum* peaking in September, *Hadrobunus fusiformis* in October, *Leiobunum bimaculatum* in November, and *Leiobunum vittatum* in December. All 5 species seem to be univoltine with a single reproductive event (indicated by the peak catch of adults), with the possible exception of *Hadrobunus fusiformis*. This species was present as adults during a long time period, from May to December, and there may be a small peak in May/June in addition to the larger autumn peak. This finding may indicate 2 generations per year. However, cursory examination of the phenology of putative immature *H. fusiformis* (data not shown) favors the univoltine hypothesis. The probable juveniles of *H. fusiformis* occur only in the cold-season samples. They appear in the late fall as the previous generation is still being captured, and start to disappear in late spring as the next generation of adults begin to appear. Those juveniles did not persist into the summer or autumn, and this finding seems to indicate a single cohort maturing primarily in the autumn. It is possible that there are 2 periods of intense activity in adults, perhaps one reflecting mating and one reflecting foraging activity. Analysis of immature size distribution would be necessary to definitively demonstrate the univoltine pattern, and we are currently working out the methodology for this.

Table 5. Phenology of harvestmen of the Savannah River Site captured by 1 year of continuous pitfall trapping, May 1995–May 1996. Total catch from 8 habitats pooled. Exact dates vary 1–2 days because only half of the habitats were sampled on a given day. Totals for each species include only adult specimens; all immature specimens pooled as "mixed immatures". The index of seasonality (I_S) was calculated for the 5 species with $n >$ number of sampling periods, 26. The index is expressed as proportion of year, with smaller proportions denoting more stenochronous species found as adults during only a short period and larger proportions represent increasingly eurychronous species. *H. f.* = *H. fusiformis*, *L. b.* = *L. bimaculatum*, *L. p.* = *L. politum*, *L. u.* = *L. uxorium*, *L. ven.* = *L. ventricosum*, *L. ver.* = *L. verrucosum*, *L. vit.* = *L. vittatum*, and *V. s.* = *L. vittatum*.

Sample	Dates (1995–1996)	*H. f.*	*L. b.*	*L. p.*	*L. u.*	*L. ven.*	*L. ver.*	*L. vit.*	*V. s.*	Mixed immatures	Total specimens	Total adults	% adults	Species present as adults
1	3–5 May	55	0	0	0	0	0	0	6	96	157	61	38.9	2
2	15–29 May	25	0	0	0	0	4	0	6	25	60	35	58.3	3
3	31 May–14 Jun	46	0	0	0	0	5	0	18	7	76	69	90.8	3
4	12–26 Jun	10	0	0	0	0	3	0	0	1	14	13	92.9	2
5	26 Jun–10 Jul	16	0	3	0	1	3	0	1	0	24	24	100.0	5
6	10–24 Jul	26	1	3	0	2	14	0	0	0	46	46	100.0	5
7	24 Jul–7 Aug	27	0	6	0	0	14	0	3	0	50	50	100.0	4
8	7–21 Aug	28	1	0	1	0	12	0	2	0	44	44	100.0	5
9	21 Aug–6 Sep	25	3	1	0	0	16	0	0	0	45	45	100.0	4
10	6–20 Sep	55	7	0	0	1	20	0	1	1	85	84	98.8	5
11	20 Sep–4 Oct	53	10	2	0	0	7	0	1	5	78	73	93.6	5
12	4–18 Oct	91	5	0	0	0	4	3	0	9	112	103	92.0	4
13	18 Oct–1 Nov	56	4	0	0	0	1	1	0	94	156	62	39.7	4
14	1–15 Nov	28	28	0	1	0	2	4	0	89	152	63	41.4	5
15	15–29 Nov	2	9	0	1	0	0	4	0	64	83	19	22.9	4
16	29 Nov–13 Dec	2	10	0	1	0	0	13	0	67	84	17	20.2	4
17	13–29 Dec	0	4	0	0	0	0	1	0	96	113	17	15.0	2
18	29 Dec–10 Jan	0	0	0	0	0	0	0	0	110	111	1	0.9	1
19	10–24 Jan	0	0	0	0	0	0	0	0	129	129	0	0.0	0
20	24 Jan–7 Feb	0	0	0	0	0	0	0	0	156	156	0	0.0	0
21	7–21 Feb	0	0	0	0	0	0	0	0	302	302	0	0.0	0
22	21 Feb–8 Mar	0	0	0	0	0	0	0	1	389	390	1	0.3	1
23	8–20 Mar	0	0	0	0	0	0	0	0	334	334	0	0.0	0
24	20 Mar–3 Apr	0	0	0	0	0	0	0	0	215	215	0	0.0	0
25	3–17 Apr	0	0	0	0	0	0	0	0	203	203	0	0.0	0
26	17 Apr–3 May	0	0	0	0	0	0	0	1	303	304	1	0.2	1
	Totals	548	82	15	4	4	105	30	40	2695	3523	828		
	I_S (months)	5.13	2.63	n/a	n/a	n/a	3.85	1.82	1.78					

The index of seasonality (Table 5) varied from highly stenochronous species with values of less than 2 months (the early maturing *Vonones sayi* and the late maturing *Leiobunum vittatum*) to over 5 months in the case of the eurychronous and possibly bivoltine *Hadrobunus fusiformis*. *Leiobunum verrucosum*, which is clearly univoltine, is also eurychronous with an I_s of almost 4 months.

Discussion

Autecology

This paper gives some of the first quantitative information about phenology and habitat distribution of the sampled species, and in general this information agrees with what we gleaned from the literature or have observed from previous collecting (M.L. Draney, pers. observ.).

Vonones sayi has been most frequently reported in soils with high sand content (well-drained), including rocky outcrops in otherwise mesic regions, sand along rivers, and semi-arid regions (Cokendolpher and Jones 1991, Goodnight 1957), and our results are consistent with this pattern. *Vonones sayi* was found at SRS in the mesic sites, which all happen to be underlain by sandy soils, although a heavier, organic-matter–rich A-horizon characterized the riparian hardwood site (1995–1996 site #7). Cokendolpher and Jones (1991) report highest adult numbers in April and May in central Texas, which is a little earlier than the late May–early June peak at SRS. In summer, both adult and immature forms have been found together in Indiana (Goodnight 1957), consistent with reports of the species living up to 3 years in the laboratory (Cokendolpher and Jones 1991).

Hadrobunus fusiformis was the most abundant species in our samples, which is extraordinary considering that the species was not described until more than a decade after our specimens were collected (Shultz 2010). The description includes 2 specimens from Aiken County, SC, but the rest of the individuals were from the mountains or near the Atlantic coast. Shultz (2010) speculated that this apparent disjunct distribution is really an artifact of sampling effort, and the present study lends support to this idea. This species was the most abundantly sampled species in our study; we trapped 548 individuals in the 1995–1996 pitfalls, which constitute 66% of total adult Opiliones. Furthermore, it is the most ecologically general of the species we sampled; it was found in all habitats sampled except for the Sandhills scrub oak–pine and the pine forest surrounding Rainbow Bay (Site #2 of 1992 survey), including both recently disturbed and old habitats, both xeric and mesic–wet habitats, and in deciduous and coniferous forests as well as field and shrub habitats. These findings indicate that it probably occurs abundantly throughout most of South Carolina. In previous collections, *H. fusiformis* tended to be most abundant in more-open and less-mature environments such as grassland and young or open woods, a habitat preference that seems to characterize other members of this genus as well (Shultz 2010). Why this species was particularly abundant at the SRS old-growth site is not known and is not clear from consideration of our data on habitat age and soil moisture; some other factors must be important.

Leiobunum bimaculatum occurs mainly on the Gulf and Atlantic coastal plains (Crosby and Bishop 1924) and is nearly at its northern limit here, except for a disjunct population in Virginia Beach, VA (Davis 1934; J.W. Shultz, pers. observ.), which might contribute to its occurrence being limited to xeric and presumably warmer locations on the SRS landscape. Most collection records of adults from other localities are in September through November, similar to the present results. Interestingly, the coloration of the population reported here is rather different from the classic coloration of the species, which is a generally dark dorsum with large bilateral white to yellow-white splotches on the carapace and first abdominal tergite. The pattern exists in the SRS populations, but the contrast of the dark and white cuticle is very reduced. Although these specimens are nearly 2 decades old, the lack of coloration is very unlikely to be an artifact of age, as the other sampled taxa do not show similar coloration changes. In any case, these specimens were killed in formalin, which preserves coloration much better than with initial immersion in ethanol (M.L. Draney, pers. observ.).

Leiobunum verrucosum is a widespread species that ranges across the eastern United States. In Maryland, it overwinters as an immature and matures in late April–early May. Adults are very abundant in June and then gradually decline throughout the summer, becoming hard to find by the end of August. However, the juveniles can be found under objects through the fall and winter (J.W. Shultz, pers. obervs.). At SRS, the species peaked much later, in mid-September. Although the seasonality of the species is very different in Maryland and South Carolina, the differences can probably be explained by the earlier autumn farther north, and suggests that the species phenology is responding to some aspect of environmental temperature. As at SRS, other known records of the species are mainly from wooded habitats. Interestingly, individuals tend to occur on plants in Maryland, but they seem to be largely ground-dwelling farther north (e.g., Ohio; J.W. Shultz, pers. obervs.).

Leiobunum vittatum is another very widespread species, ranging up the Atlantic coast from Florida to Canada and west to the Great Plains, and even further west in the south (Cokendolpher and Lee 1993). It is a common "late season" form (it peaked latest of all SRS species) that is often very abundant. It inhabits a wide range of habitats but prefers taller woody vegetation (bushes and trees). The sudden appearance of this species late in the season at SRS likely reflects (1) the climbing habits of immatures (J.W. Shultz, pers. obervs.) and (2) the elimination of ground-living competitors late in the season. Subadults of the species are easy to diagnose, and we recorded none, even from the habitats where the 30 pitfall individuals were found. The behavior of the immatures might account for this.

Leiobunum vittatum serves as a reminder that the habitat distribution of each species needs to be taken into a regional context. In the present study, *L. vittatum* seems to be restricted to the oldest and most mesic of the habitats at SRS (Table 3), yet the species seems to be more broadly distributed, including within more-xeric old field and young forest habitats, farther north in its range (e.g., Wisconsin; M.L. Draney pers. observ.).

In Eupnoi Opiliones in general, sexual maturation is usually delayed for some time (up to several weeks) after the final molt (J.W. Shultz, pers. obervs.). Therefore, sudden, delayed appearance in pitfalls may reflect males searching for females and females looking for oviposition sites. The fact that *L. vittatum* seems to show up suddenly (Table 5) may be an illustration of this delayed maturation phenomenon.

Leiobunum politum Weed is generally a woodland or edge species in mesic environments. Like *L. vittatum*, it is very widespread in eastern North America. The species can be found on both the ground and low vegetation, but individuals are not found on tree trunks (J.W. Shultz, pers. obervs.).

Finally, *Leiobunum ventricosum* (Wood) and *Leiobunum uxorium* Crosby and Bishop are both climbing species, which accounts for their rarity in SRS pitfall samples. It is likely that the biology of many "long-legged" harvestman species will lead to biases in species representation using pitfall sampling. These species probably spend a good deal of time foraging and resting on elevated surfaces and may spend limited time on the ground where they are vulnerable to trapping.

Faunistics

Our additions bring the total Opiliones species recorded from South Carolina to 20 (including 3 undescribed species; Table 1). The 9 species we found on the site represent over 40% of the state's known fauna. Figure 1 highlights the fact that the state's Opiliones fauna remains very poorly known. Harvestmen records are reported from only about one third (17 of 46) of South Carolina counties, and *Vonones sayi*, a distinctive species that may be common in a variety of South Carolina habitats (M.L. Draney, pers. observ.), is here reported from the state for the first time.

This list should not be considered in any sense a complete checklist for the Opiliones of the SRS, because the great majority of the sampling was done using one method, pitfall traps. While pitfall traps are highly effective at determining "activity density" (i.e., number of active individuals encountered in an area during the sampling period) of species that wander across the ground surface, they certainly undersample and may fail to sample both smaller soil- and litter-dwelling species as well as species that predominately inhabit vegetation. While we did collect some of these species (for example, the soil-dwelling *Vonones sayi* and the largely climbing *Leiobunum uxorium*, *L. ventricosum*, and *L. vittatum*), there are very likely other species in these categories on the site. Also, sampling was focused on a relatively small number of sites (over 98% of the specimens from the eight 1995–1996 habitats, plus limited sampling from 5 other sites), and while these sites were selected to both represent the most common habitat types on the site and to cover the range of habitat types from xeric to wet–mesic, not all habitats were thoroughly sampled. In particular, there was relatively little sampling in wetland areas (other than our Rainbow Bay and mixed swamp forest sites). Future work in this region should focus on vegetation sampling, especially of forest canopies, and expand to include other habitats and microhabitats, especially wetlands and more emphasis on small litter-dwelling species.

Our attempts to estimate species richness, however, showed that our 1995–1996 pitfall samples did an adequate job of sampling the ground-active opilionid fauna. With our overall pitfall data, there were no singletons or doubletons; the rarest species (*L. uxorium* and *L. ventricosum*) were each represented by 4 individuals. This pattern largely held in estimates of individual habitats as well; there were no doubletons in individual habitat data, and only the riparian hardwood and riparian old-growth sites had any singletons (1 species each). Since adequately sampled communities are composed of species which have all been sampled multiple times, we can be fairly confident that we sampled most of the ground-active species in most of the habitats (with the possible exception of the 2 very diverse riparian sites). Overall, our results lend support to the idea that pitfall trapping is a good method for sampling ground-level Opiliones. The 1995–1996 pitfall samples yielded 8 of the 9 species recorded from SRS, including all species except *Bishopella laciniosa*, a rarely collected species known from only 2 other instances in South Carolina (Fig. 1).

Our 1995–1996 pitfall data is one of the most intensive sample sets in the literature for ground-dwelling Opiliones. Only a few other large systematic sampling efforts have been conducted (Bachmann and Schaefer 1983, Curtis 1978, Jennings et al. 1984), and the present results show that these systematic efforts can improve our understanding of the distribution and phenology of harvestman species. In addition, our data set can be used to assess the value of the less-intensive sampling we also conducted at SRS. It is apparent that less-intensive surveys do not yield as many species, but are generally adequate for documenting the most abundant species on a site. The 1992 survey (n = 73 individuals) yielded 5 of the 9 recorded species, including all species making up 4% or more of the 1995–1996 intensive pitfall series (40 or more of n = 828 pitfall individuals). More-intensive sampling of a few sites and extensive sampling across the landscape will be needed to come to a detailed understanding of the ecology of North American harvestmen.

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Literature Cited

Bachmann, E., and M. Schaeffer. 1983. The opilionid fauna of a beech wood and dry grassland on limestone (Arachnida: Opilionida). Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg 26:141–149.

Bishop, S.C. 1949. The Phalangida (Opiliones) of New York with special reference to the species of the Edmund Niles Huyck Preserve, Rensselaerville, New York. Proceedings of the Rochester Academy of Science 9:159–235.

Chao, A. 1987. Estimating the population size for capture–recapture data with unequal catchability. Biometrics 43:783–791.

Chao, A., R.L. Chazdon, R.K. Colwell, and T.-J. Shen. 2005: A new statistical approach for assessing compositional similarity based on incidence and abundance data. Ecology Letters 8:148–159.

Clouse, R.M., and W.C. Wheeler. 2014. Descriptions of two new, cryptic species of *Metasiro* (Arachnida: Opiliones: Cyphophthalmi: Neogoveidae) from South Carolina, USA, including a discussion of mitochondrial mutation rates. Zootaxa 3814:177–201.

Cokendolpher, J.C. 1980. Replacement name for *Mesosoma* Weed, 1892, with a revision of the genus (Opiliones, Phalangiidae, Leiobuninae). Occassional Papers, Museum of the Texas Tech University 66:1–19.

Cokendolpher, J.C., and S.R. Jones. 1991. Karyotype and notes on the male reproductive system and natural history of the harvestman *Vonones sayi* (Simon) (Opiliones, Cosmetidae). Proceedings of the Entomological Society of Washington 93:86–91.

Cokendolpher, J.C., and V.F. Lee. 1993. Catalogue of the Cyphopalpatores and Bibliography of the Harvestmen (Arachnida, Opiliones) of Greenland, Canada, USA, and Mexico. Vintage Press, Lubbock, TX.

Colwell, R.K. 2013. EstimateS: Statistical estimation of species richness and shared species from samples. Version 9. User's Guide and application. Available online at http://purl.oclc.org/estimates. .

Crosby, C.R., and S.C. Bishop. 1924. Notes on the Opiliones of the southeastern United States, with descriptions of new species. Journal of the Elisha Mitchell Scientific Society 40:8–26.

Curtis, D.J. 1978. Community parameters of the ground layer araneid-opilionid taxocene of a Scottish island. Symposia of the Zoological Society of London 42:149–159.

Davis, C.E., and L.L. Janacek. 1997. DOE Research Set-Aside areas of the Savannah River Site. SRS/National Env. Research Park Program Publication SRO-NERP-25. Savannah River Ecology Laboratory, Aiken, SC.

Davis, N.W. 1934. A revision of the genus *Leiobunum* (Opiliones) of the United States. American Midland Naturalist 15:662–705.

Draney, M.L. 1997. Diversity and life-history variation among ground-dwelling Linyphiidae (Araneae). Ph.D. dissertation, University of Georgia, Athens, GA.

Draney, M.L., and D.A. Crossley Jr. 1999. Relationship of habitat age to phenology among ground-dwelling Linyphiidae (Araneae) in the southeastern United States. Journal of Arachnology 27:211–216.

Goodnight, C.J. 1957. Two representatives of a tropical suborder of opilionids (Arachnida) found in Indiana. Proceedings of the Indiana Academy of Science 67:322–333.

Gorsuch, C.S., G.T. Lee, and D.R. Alverson. 1989. Arthropod species collected from peach trees in South Carolina utilizing a whole-tree sampling method. Journal of Agricultural Entomology 6:233–255.

Hoffman, R.L. 1955. Distributional records for some scarce phalangids in the southern Appalachians. Journal of the Elisha Mitchell Scientific Society 71:17–19.

Holsinger, J.R., and S.B. Peck. 1971. The invertebrate cave fauna of Georgia. Bulletin of the National Speleological Society 33:23–44.

Ingianni, E.A., C.R. McGhee, and J.W. Shultz. 2011. Taxonomy of the *Leiobunum calcar* species-group (Opiliones: Sclerosomatidae: Leiobuninae). Journal of Arachnology 39:454–481.

Jennings, D.T., M.W. Houseweart, and J.C. Cokendolpher. 1984. Phalangids (Aranchida: Opiliones) associated with strip clearcut and dense spruce–fir forests of Maine. Environmental Entomology 13:1306–1311.

McGhee, C.R. 1970. The sacculate and lanceolate groups of the genus *Leiobunum* (Arachnida: Phalangida, Phalangiidae) in eastern North America. Ph.D. Dissertation. Virginia Tech, Blacksburg, VA.

Pinto-da-Rocha, R., G. Machado, and G. Giribet (Eds.). 2007. Harvestmen: The Biology of Opiliones. Harvard University Press, Cambridge, MA. 597 pp.

Shear, W.A. 1986. A cladistic analysis of the opilionid superfamily Ischyropsalidoidea, with descriptions of the new family Ceratolasmatidae, the new genus *Acuclavella*, and four new species. American Museum Novitates 2844:1–29.

Shultz, J.W. 2010. A new species of *Hadrobunus* (Opiliones: Sclerosomatidae: Leiobuninae) from the southeastern United States. Journal of Arachnology 38:572–580.

Shultz, J.W. 2012. The identity of *Hadrobunus grandis*: reassignment of *Leiobunum aurugineum* to *H. grandis* and *H. nonsacculatus* new species (Opiliones: Sclerosomatidae: Leiobuninae). Journal of Arachnology 40:296–303.

Workman, S.W., and K.W. McLeod. 1990. Vegetation of the Savannah River Site: Major community types. SRO-NERP-19. A publication of the Savannah River Site, National Environmental Research Park Program, Aiken, SC.

World Meteorological Organization. 2016. WMO frequently asked questions: What is climate? http://www.wmo.int/pages/prog/wcp/ccl/faqs.php. Accessed 21 July 2016.