Ecological Observations of the Trapdoor Spider *Myrmekiaphila comstocki* Bishop & Crosby 1926 (Araneae, Mygalomorpha, Euctenizidae, Apomastinae) in the Ouachita Mountains of Arkansas

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Cover Photograph: Adult male of the trapdoor spider *Myrmekiaphila comstocki* from the Ouachita Mountains Biological Station. 2017 photograph © Laurence Hardy.

Ecological Observations of the Trapdoor Spider *Myrmekiaphila comstocki* Bishop & Crosby 1926 (Araneae, Mygalomorpha, Euctenizidae, Apomastinae) in the Ouachita Mountains of Arkansas

Laurence M. Hardy*

Abstract - This study focused on the ecology of the trapdoor spider *Myrmekiaphila comstocki* in the Ouachita Mountains of west-central Arkansas in order to better understand the microhabitat of the burrows and the activity season of this species. I studied a population of 56 individually marked burrows during 2003–2009 at the Ouachita Mountains Biological Station. I recorded the surface structure of the burrows, temperatures, burrow depth, microhabitat around the burrow, and the facing direction of the trapdoor relative to the surrounding terrain. Spiders were active in all seasons and at ground surface temperatures that were below freezing; however, the bottoms of the burrows were never below freezing. Burrow diameters change over time, apparently due to the growth of the spider as the burrow widths appear to be correlated to the size of the spider inhabitants. The burrows were 60–330 mm deep and were open 25% of the time. Larger burrows were destroyed (by possible predation or other physical damage) more often than were smaller burrows. The population density in the area studied was 366 burrows per hectare.

Introduction

Myrmekiaphila comstocki Bishop & Crosby (Araneae, Mygalomorpha, Euctenizidae) is the only species within its genus that has a geographic distribution west of the Mississippi River; the species is found in the Ouachita Mountains, the southwestern half of Arkansas, southern Oklahoma, northeastern Texas, and northern Louisiana (Bond and Platnick 2007). The only other *Myrmekiaphila* species with as large a geographic distribution is *M. foliata* Atkinson, which is found throughout the Appalachian Mountains westward to the eastern edge of Mississippi (Bond and Platnick 2007); neither species is known to be widespread in Mississippi. However, *M. comstocki* is locally abundant on the Ouachita Mountains Biological Station (OMBS), in the Ouachita Mountains of Arkansas, but is not commonly found in much of its geographic distribution, probably due to its fossorial and sedentary habits. Females reside for almost their entire lives in vertical, silk-lined burrows in the ground, which they probably repair and enlarge in order to accommodate their increasing body size (Costa and Conti 2013). Structural adaptations of the females for burrowing include shorter legs than those of males, a rastellum on the chelicerae, uniform brownish-tan coloration, a uniformly sclerotized carapace, and

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*Ouachita Mountains Biological Station, 281 Polk Road 615, Mena, AR 71953, and the Museum of Life Sciences, Louisiana State University in Shreveport, One University Place, Shreveport, LA 71115-2399; lhardy@lsus.edu.

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a paucity of setae on legs and body. The secretive males are rarely found, and their retreats are not well known; most males have been seen while the spider was moving about on the substrate surface.

In 2000, I deiscovered numerous burrows of *Myrmekiaphila comstocki* in the immediate proximity of several of the buildings at the OMBS. I have verified at least 2 other species of mygalomorphs—*Ummidia audouini* (Lucas) and *Aphonopelma hentzi* (Girard)—from the OMBS. In the course of capturing a few specimens for a representative spider collection, I realized that *M. comstocki* was abundant: 20 burrows were located in an area of only 5–6 m in diameter. Later that year, during the coldest part of the winter, I discovered a few burrows with their trapdoors open. A brief census over several nights revealed that many spiders were active with open burrows, frequently with the resident spider visible in the entrance of the open burrow. In some cases, there were patches of snow near the open burrow. Is this species active throughout the year? Is it feeding during the winter? Is the bottom of the burrow warmer than the surface air temperature? Does an individual spider change the size of the burrow and the trapdoor as it grows? Do the trapdoors open toward a particular direction? Was there any physical relationship between the burrow and any nearby plants, rocks, or sticks? These many intriguing questions about their unusual activity pattern, their apparent abundance, the paucity of information reported about their ecology, and the possibility of geographic variation in some interesting ecological parameters prompted my subsequent efforts to collect ecological data for this species, especially during the winter.

Spider activity in winter conditions of freezing, or near-freezing, temperatures has been reported by several observers. Aitchison (1984a) reported at least 54 winter-active species that can occur in all the classes of phenology except the strictly annual, autumn-stenochronous species with overwintering eggs in southern Canada; however, no mygalomorphs were included. Aitchison (1984b) found many species of spiders active and feeding at temperatures of 5 ºC or lower; again, none were mygalomorphs.

Atkinson (1886b:131, 132) provided the original description of the genus *Myrmekiaphila* and of the species *M. foliata*, as well as information on burrows of *M. foliata* that included drawings of the interior doors and chambers from near Chapel Hill, NC (Atkinson 1886b:113). He also gave information about the burrow structure in the natural environment. Atkinson (1886a) described the construction, in captivity, of several tubes of a trapdoor spider, probably of *M. foliata*, which he had described in the same month (Atkinson 1986b), and the only species of the genus in North Carolina (Bond and Platnick 2007). Pocock (1902) does not include a single scientific name in his article; however, he does include many accurate pieces of information, some drawings that show detailed structure of trapdoor burrows, presumably from field observations, and even a brief account of the purseweb spiders of the genus *Sphodros*. Savory (1926) distinguished between mygalomorphs with hunting versus burrow-digging habits. Gertsch and Wallace (1936) described *M. torreya* Gertsch and Wallace from the Florida panhandle and illustrated the burrow as having an interior branch closed with a hinged trapdoor and an outer trapdoor that was hinged on the uphill side. They reported a density of about 1 burrow per square meter, with the greatest concentration "on leaf-mould covered slopes" (Gertsch and Wallace 1936:15), usually open both day and night, and they found only 1 male in a collection of over 200 females. When I measured the slope of the burrow opening shown in their illustration (fig. 5) it appeared to b 32° from horizontal. Hunt (1976) observed *Myrmekiaphila* burrows in the same sandy-clay soil habitat as *Antrodiaetus* in Georgia and a specimen of *Myrmekiaphila* that constructed a burrow in captivity and later emerged as a mature male on 3 November.

The excellent study of the ecology of *Aliatypus* (Antrodiaetidae) from California and Arizona by Coyle and Icenogel (1994) demonstrated the use of ecological data combined with morphological data to support phylogenetic analyses. Most of the several species they studied were in arid environments and constructed burrows on north-facing slopes at greater than 45° from horizontal. The longest burrows they reported were 51 mm and were located in the driest desert in the geographic distribution of *Aliatypus*. Bond and Coyle (1995) reported many aspects of the natural history of a trapdoor spider (probably *Ummidia rugosa* Karsch) for a Costa Rican population. Their study suggests considerable geographic variation in the microhabitat preferences of *Ummidia*, from steep earthen banks, preferred by most *Ummidia* species, to level to gently sloping ground, preferred by *Ummidia* in western North Carolina. *Sphodros rufipes* (Latreille) in northwestern Louisiana used only hardwood trees for its vertical webs, and none were found on pines, even though pines were equally abundant in the habitat (Hardy 2003). Poteat (1889), however, reported on a large population of *Sphodros* (probably *S. rufipes*; see Hardy 2003) in North Carolina that used 28 pines but only 2 hardwoods for its web support. These results suggest geographical variation in ecological parameters of spiders.

Ballooning of young mygalomorphs in nature was recorded for *Ummidia carabivora* (Atkinson) by Baerg (1928) and for *Sphodros* by Coyle (1983). Chamberlin and Ivie (1945) provided some ecological data on the burrows of *Antrodiaetus*. Another mygalomorph (*Atypoides* [= *Antrodiaetus*] *hadros* (Coyle)) has been recorded in southern Missouri, close to Arkansas and the Ouachita Mountains (Coyle 1968). Studies of *Cyclocosmia* in Georgia reported measurements of the degree of slope of the terrain and soil composition in which burrows were found, and that *Myrmekiaphila comstocki* also occurred in the vicinity (Hunt 1976). Gertsch and Platnick (1979) reported ecological observations for Mecicobothriidae, which are non-burrowers. Studies by Gertsch and Platnick (1980) on the tubes of *Sphodros* contributed to the ecology of that genus as did Beatty's (1986) discovery of tubes of *S. rufipes* constructed horizontally, above ground, in an island habitat with dry, hard, and rocky soil. However, it is not uncommon that original descriptions of very rare mygalomorphs (2 tropical species in the Actinopodidae by Platnick and Shadab [1981], 3 new South American species of *Striamea* by Raven [1981] and Dipluridae by Raven [1981]) contain very little, if any, information on ecological parameters. In Raven's (1980) review of the Hexathelidea, which contains burrowers, little ecological information is given. Raven (1985) summarized some ecological information for the non-burrowers of the Cyrtaucheniidae. *Microhexura*

Crosby and Bishop, a non-burrowing mygalomorph, is active in very cold weather (Coyle 1981).

Hedin and Bond (2006) provided a major summary of molecular phylogenetics of the Mygalomorphae using rRNA data, and their dataset included the genus *Myrmekiaphila* but not the species studied herein. The systematic revision of *Myrmekiaphila* by Bond and Platnick (2007) does not include information on behavior or ecology for *M. comstocki*, except for the delineation of the geographic distribution west of the Mississippi River (all other known species of the genus are east of the Mississippi River). The collection locality of their 2 samples was in the watershed of the Little Missouri River, in the Caney Creek Wildlife Management Area, adjacent to the Caney Creek Wilderness, located 2.0 miles west and 3.0 miles south of my study site, which is in the watershed of the Ouachita River. Bailey et al. (2010) reported on molecular data for 9 species of *Myrmekiaphila*, including *M. comstocki*, the subject of this paper. Their samples of *M. comstocki* were the same as those of Bond and Platnick (2007) and showed that *M. comstocki* can be diagnosed, genetically, on the basis of a single unique 12S/16S nucleotide substitution, G(108), and appears to be very close to the ancestral condition of the genus. No ecological data were included in their analysis. However, the reconsideration of *Myrmekiaphila* systematics (Bond et al. 2012b) which placed *Myrmekiaphila* in the family Euctenizidae, reported that males of their newly described species, *M. tigris* Bond and Ray, were found wandering on warm, damp mornings during December and January in Alabama and Georgia; females were collected from 6–8-cm-deep burrows, some with below-ground side chambers and trapdoors. The preferred tree topology based on Bayesian analysis of the 12S/16S mDNA data set (Bond et al. 2012a) shows *M. comstocki* as paraphyletic (note position of MY 3366) but also as the most basal, possibly most ancestral, of all species of *Myrmekiaphila*. If confirmed, this finding would suggest that ancestral and allopatric populations of *M. comstocki* dispersed eastward across the Mississippi River, eventually producing the speciation events that resulted in the remaining descendant species of the genus.

There is a need for systematic studies of spiders that include ecological parameters. It is now well known that ecological requirements of species are regulated by natural selection and are an integral part of their evolutionary history (Foster and Endler 1999, Slobodkin 1961). Moore (1944, 1946, 1947) pointed out the possibility of geographic variation in reproductive biology in the *Lithobates pipiens* (Schreber) (= *Rana pipiens*) complex, and those studies set the stage for the rapid increase in our knowledge of the systematics of frogs of the genus *Lithobates*. Geographic variation was reported in some ecological parameters of 4 bisexual and a unisexual species of Brazilian lizards (Teidae) by Mesquita and Colli (2003) and among some populations of the parthenogenetic *Aspidoscelis tessellatus* (Say, in James), *A. neomexicanus* Lowe and Zweifel, and others (Cole et al. 1988, Dessauer and Cole 1989, Zweifel 1965). The above material is relevant for autecology studies.

The complex of demes that comprises the geographic distribution of a species includes all of the peripheral populations of that species. The peripheral populations

(= demes) are exposed to the selection pressures of their local environments, and those selection pressures can vary greatly from one adjacent peripheral population to the next around the boundary of the species. These peripheral populations are more likely than more-interior populations to become allopatric and, as such, become the possible progenitors of future speciation events.

The inclusion of ecological data from throughout the geographic distribution of a species in order to contribute to our knowledge of the geographic (and possibly genetic) variation in ecological parameters is almost impossible to attain at one time in a single project; however, each deme with such data is a single piece of a larger evolutionary scenario. Therefore, as ecological data of populations are acquired by individual projects, sometimes over long periods of time, we might detect important, previously unknown, evolutionary trends and relationships (e.g., the history of *Lithobates* systematics) that will strengthen other systematic studies.

The study site for this population of *M. comstocki* is at or near the northeasternmost known edge of the geographic distribution of the species (Bond and Platnick 2007) and, therefore, probably reflects characteristics of a peripheral deme for the species. The approximate center of the species geographic distribution is ~300 km to the southwest (near the Dallas–Ft. Worth, TX, area). The OMBS population could be considered a peripheral population of the species and, as such, (1) carries only a fraction of the total genetic variability of the species, (2) is exposed to marginal environmental conditions, and (3) is exposed to severe natural selection due mainly to density-independent factors. Reduction of gene flow (due to an increase of unidirectionality for a peripheral population) and depletion of genetic variability results in different selection pressures than those experienced by more-central populations and the possibility of a shift into different ecological niches (Mayr 1963).

Characteristics of peripheral populations that can be tested on a deme-by-deme basis include the geographic location of the peripheral population in the total geographic variation of the species, and other variables such as, extent of geographic isolation, population density, individual variation, polymorphism, gene flow, and several other characteristics of genetics, ecology, and morphology. Rare in published lists of characteristics of peripheral populations are any aspects of ecological parameters that can be compared to other populations within the species geographic distribution, especially with regard to peripheral versus central populations.

Characteristics resulting from this study of a peripheral population that can eventually be compared to other demes in the species distribution include: microhabitat parameters, placement of the trapdoor relative to the surrounding terrain, extent of loss (depredation), composition of predator community, temperature tolerance, depth of burrow, daily and seasonal activity patterns, and the size of the trapdoor hinge (as a measure of burrow size and spider size). Addition of geographic variation of objective ecological/behavioral data will add a new dimension to comprehensive systematic studies and eventually broaden our understanding of the genetic relationships and evolutionary histories of these taxa.

This 6-year study adds more to our basic ecological knowledge of this interesting spider. The main objective of the study of this local population was to measure several aspects of some ecological parameters, for example, when the spiders were active during the year, temperatures in and around the burrows, the orientation of the open trapdoor relative to the immediate slope of the ground, the microhabitat of the immediate vicinity of the burrow trapdoor, the changes in size of the trapdoor, the associated weather conditions and time of day when trapdoors were open, how long individual burrows were used, and the failure rate of burrows.

Field-Site Description

I conducted this study on the Ouachita Mountains Biological Station (34.461°N, 93.998°W, elevation = 365.8 m; in WGS 84), about 2 miles west and 2 miles south of Big Fork, Polk County, AR. The study site was in the vicinity of the headquarters buildings of the OMBS and in second-growth *Quercus* (oak)–*Carya* (hickory) forest. The forest floor contains moderate vegetation, including *Vaccinium* spp., *Cornus florida* L. (Flowering Dogwood), *Toxicodendron radicans* (L.) Kuntze (Poison Ivy), and some grasses (MacRoberts et al. 2005). The population of *M. comstocki* was on a ridge, sloping down toward the north, with sides sloping to the west and to the east. The substrate was coarse rocky soil, and there was no standing water within 100 m from the study site.

Methods

To mark the individual spider burrows reliably without disturbing the burrow or the spider from the initial marking through the end of the study, I devised the following method. I taped a compass to one end of a 30-cm-long fiberglass rod (Fig. 1A). When a burrow was to be marked, I positionsed the fiberglass rod (representing the radius of a circle) so that the burrow was at the compass end of the rod (Fig. 1B), then moved the non-compass end of the rod left or right (keeping the compass end stationary over the burrow) along an arc until the compass needle was at 180° and the rod was still positioned at the edge of the burrow. Next, I inserted a wire engineering flag bearing the burrow number into the ground at the non-compass end of the fiberglass rod (to reduce any effect of the iron wire on the compass; Fig. 1F). This put the flag exactly 30 cm north (0° azimuth) of the burrow (Fig. 1F). Finally, I carefully drove a plastic survey stake into the ground adjacent to the wire and with the face of the stake toward the burrow and centered on the wire. Later, to find the burrow (even when it was closed and well-camouflaged; Figs. 1C, 2) I placed the non-compass end of the fiberglass rod against the center of the stake and moved the compass end of the rod until the compass needle was at 180°. The burrow would be at the compass end of the rod (Fig. 1A, B). This method allowed me to accurately identify burrows just a few centimeters apart and to recognize a marked burrow from a new one in very close proximity. All of the burrows were very difficult to recognize when the trapdoor was closed (Figs. 1D–E, 2). Tests of this system correctly distinguished objects as close as 1 cm apart. I placed the burrow identification flags prior to December of 2003 and recorded the first observations on 3 December 2003 and the GPS data on 30 April 2004. The last observation day for this study was 17 March 2009.

Microhabitat parameters included the distance (cm, distances greater than 1 m were recorded as 101 cm) from the burrow to the closest dicotyledonous plant, monocotyledonous plant, moss, and exposed rock surface (greater than 1 cm diameter). The top of the trapdoor was recorded as open, closed, damaged, or missing. When recording the compass direction (azimuth degrees) that the inside surface of the open trapdoor faced, I considered trapdoor azimuths of 316º–360º and 0º–45º to be the north quadrant, 46º–135º to be the east quadrant, 136º–225º to be the south

Figure 1. (A) Fiberglass rod and compass used to locate individual burrows of *Myrmekaiphila comstocki* with good precision. Small arrows indicate the burrow trapdoor at the front end of the fiberglass rod; note that the compass needle is on zero degrees and the back end of the rod is against the wire of the marker flag (an orange survey stake had not yet been placed at this burrow, number 17). (B) Detail of fiberglass rod at edge of burrow trapdoor; arrows indicate edge of trapdoor. (C) Same as (B), without rod or arrows. (D) A closed burrow. (E) Same burrow as in (D) with arrows indicating edge of burrow. (F) A closed burrow with locator rod in place. Scale bars = 2.5 cm.

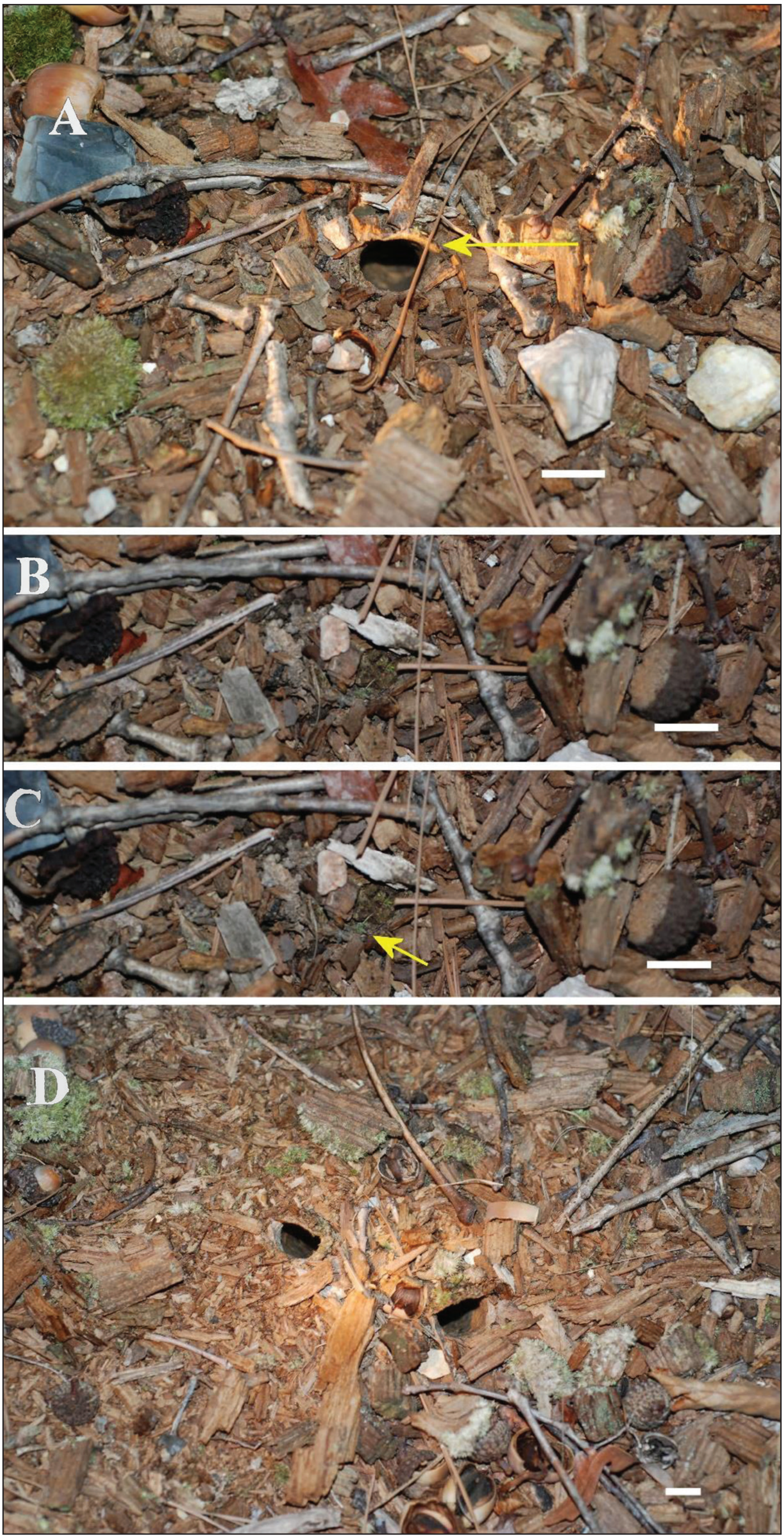

Figure 2. Open and closed burrows of *Myrmekaiphila comstocki*. (A) An open burrow, the arrow indicates the right side of the hinge. (B) A closed burrow. (C) The closed burrow in (B) with an arrow pointing to the edge of the trapdoor away from the hinge. (D) Two open burrows. Scale bars = 2.5 cm.

quadrant, and 226º–315º to be the west quadrant. The north quadrant degrees were adjusted as positive or negative around 0º to correct statistical calculations. I also recorded the compass direction of the downhill slope of the ground from the inside face of the open trapdoor.

The length (mm) of the trapdoor hinge was measured at the junction with the burrow wall. In order to reduce disturbance to the spider, I took this measurement only a few times during the study, and only when the trapdoor was open and undamaged (the hinge could not be accurately measured when the trapdoor was closed). The number of observations for each burrow varied because of natural burrow destruction that occurred during the study.

I took soil samples at a depth of 10 cm adjacent to active burrows that were not marked as part of this study. Each sample was oven-dried to determine water content and then processed through standard soil sieves to obtain proportions of particle sizes.

At the beginning of each observation period, I recorded weather conditions that usually included the air temperature 1 m above the burrow, the air temperature 1 cm above the burrow, and the temperature of the soil surface within a few centimeters from the burrow (on bare soil). I also recorded notes about the wind (presence and general strength), percent of cloud cover, presence of precipitation, or any thunder or lightning. Weather conditions for the study area (Table 1) were taken from the Big Fork 1 SSE, AR, station (NOAA) located at the OMBS.

To measure the temperature at the bottom of a burrow, I inserted a tiny thermistor, 2 mm in diameter, into an open burrow until it touched the bottom (with very gentle pressure). After recording the temperature at the bottom of a burrow, I grasped the thermistor wire at the surface of the ground and withdrew it, measuring the length from the ground surface to the thermistor tip to record the depth of the burrow. Because each burrow measured was closed and open on subsequent nights, I concluded that the temperature measurement had done little disturbance to the resident spider. The burrow depth was measured only 1 time for each burrow and at the same time when the temperatures were recorded (see above). The temperature of the adjacent ground surface was measured continuously using I-buttons (Maxim Integrated, DS1921G) that were positioned on the ground surface within a few cm

Table 1. Temperature and precipitation weather data recorded during the project; NOAA, Annual Climatological Summaries for Station ID 030664, Big Fork 1 SSE, AR, US. Temperature was not recorded at that station during 2003 and 2004.

Year	Mean temp. (°C)	Min temp. (°C)	Date of min temp.	Max temp. (°C)	Date of max temp.	Precipitation (inches)
2003	-	-	-	-	-	52.9
2004	-	-	-	-	-	67.0
2005	16.9	-12	10 Dec	35.6	23 Jul, 22 Aug	33.1
2006	15.9	-14	8 Dec	38.3	20 Jul	56.3
2007	15.8	-17	16 Feb	38.3	14 Aug	63.6
2008	14.9	-12	22 Dec	37.2	3 Aug	83.8
2009	14.6	-10	10 Dec	37.8	16 Jul	84.6

of the entrance of Burrow 35 (Fig. 3), which was active during the entire study period, and covered with a piece of bark to provide shade. The parameters used for setting the I-buttons varied during the project to obtain as much detail as possible.

For each observation, I noted whether the trapdoor was closed or open and if the spider was present (visible in the entrance of the open burrow). An open and undamaged trapdoor with a visible spider indicated that individual was active; a closed trapdoor indicated that the resident spider was inactive at that time; and a damaged trapdoor suggested predation, death, or dispersal. I considered the spider to have been temporarily inactive if the trapdoor was closed or damaged and subsequently found to be open and undamaged (repaired) during a later observation. If a trapdoor was damaged and the burrow was filled or obliterated, I considered the burrow to be vacated. I estimated the population density by measuring the rectangular area that enclosed all burrows studied and converting that value to the number of burrows per hectare.

Results

I took a total of 628 data points for 58 burrows on 35 different nights beginning on 3 December 2003 and ending on 17 March 2009 (a total of 1931 days; Fig. 4). The number of observations per night decreased from the original 58 burrows to a maximum of 38 burrows at the end of the study, due to loss of burrows because of depredation or other damage. The physical locations of the burrows in the study area were in 2 clusters (Fig. 3) with a 2-m-wide trail between them in a SSW to NNE direction.

Size

Two adult males and 9 adult females were collected a short distance away from the study population during an on-going spider survey of the OMBS (all preserved specimens are in the spider collection of the Museum of Life Sciences of Louisiana State University in Shreveport, Shreveport, LA). Those preserved specimens were gently blotted to remove excess alcohol and weighed to the nearest 0.0001 g on an analytical balance, and their volumes were measured to the nearest 0.01 ml by volume displacement. The 2 males weighed 0.4664 g and 0.5174 g and had respective volumes of 0.70 and 0.50 ml. The mean weight of the 9 females was 0.5036 g (0.1671–0.9715) and mean volume was 0.53 ml (0.20–1.00, Fig. 5). The regression line (Fig. 5) suggests that there is little, if any, ontogenetic change in shape that would be reflected in changes of mass or volume, even from the smallest to the largest spider in the sample.

Figure 3 (following page). Map of trapdoor spider burrows in the study area; north is at the top. Closed circles represent active burrows throughout the study; open circles represent burrows that were lost (predation, physical damage, or unknown) before the end of the study; numbers are individual burrow identifications. GPS data was recorded on 28 August 2004 (1930 h). A trail ~2 m wide aligned by burrows 19, 20, and 28 separated the population into 2 groups which were not analyzed separately.

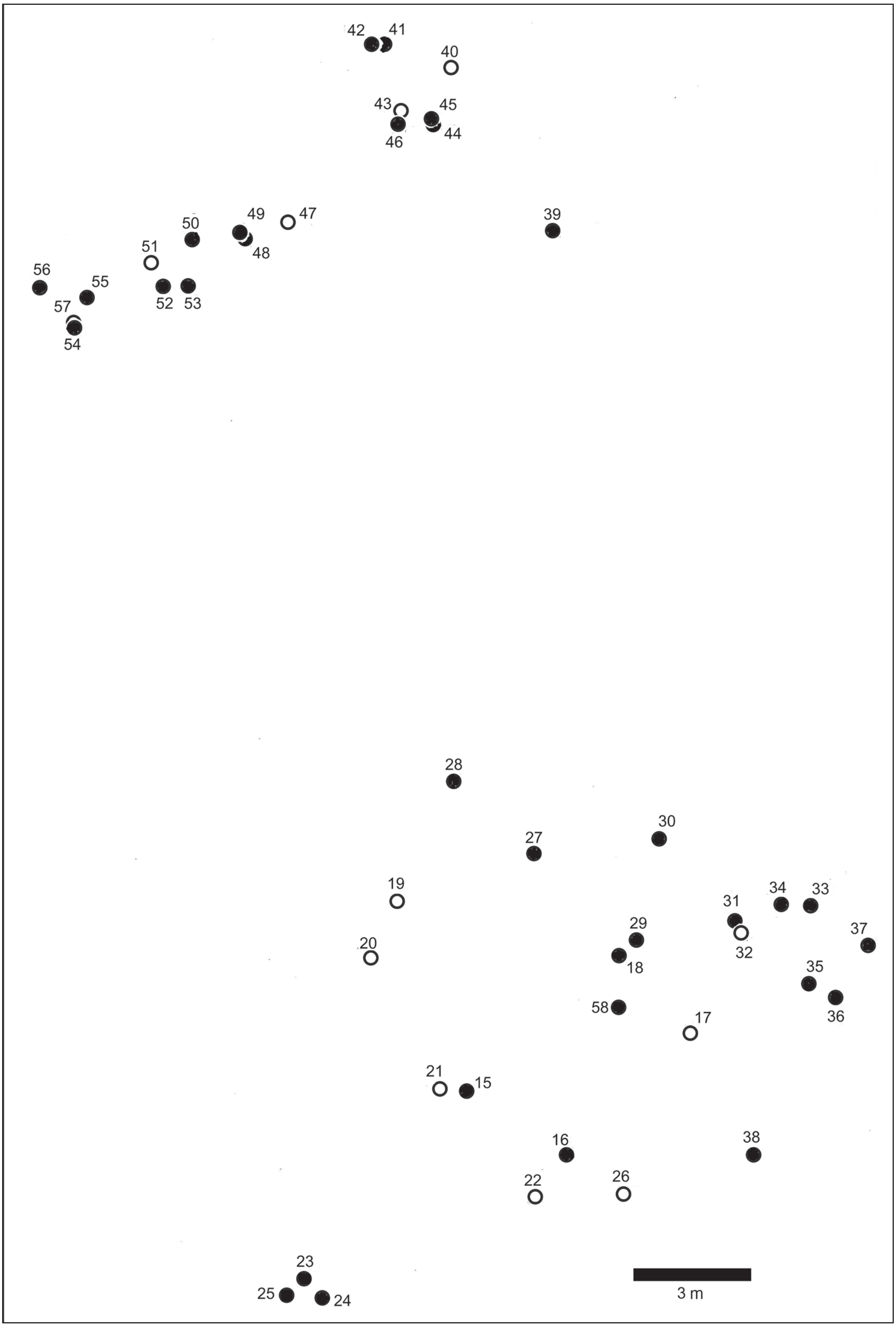

Figure 3. [Caption on previous page.]

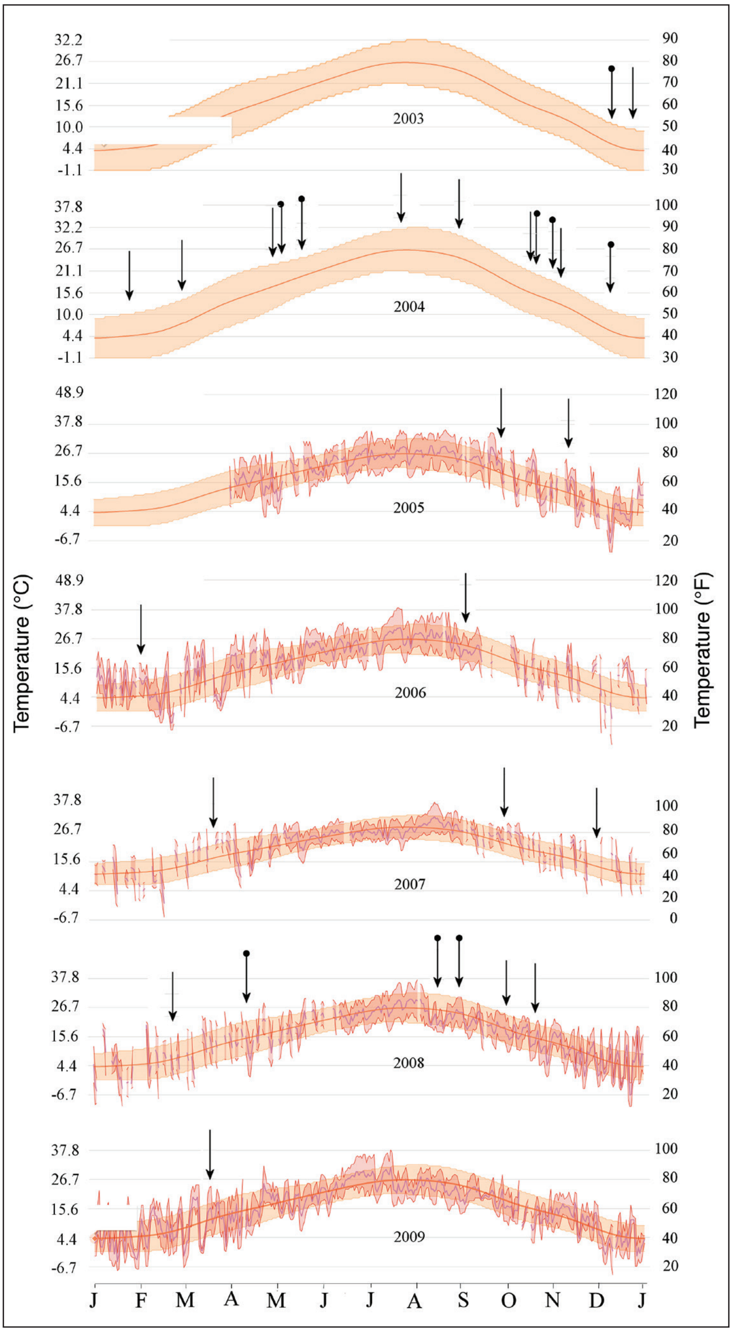

Figure 4. The pattern of air temperatures recorded at the OMBS (NOAA, Station ID=030664; Big Fork, 1 SSE, AR, US) during 2003–2009. Temperature records for this station, at this location, were initiated in early 2005. The highest mean temperature was 16.91 °C (62.43 °F) in 2012, the lowest mean was 13.76 °C (56.77 °F) in 2014, the mean temperature in 2003 was unknown, and the mean temperature in 2009 was 14.86 °C (58.74 °F). The graph lines shown in part of 2005 and 2006–2009 are daily maximum (above), mean (middle), and minimum (below); gaps represent dates for which temperature data were not available. The letters at the bottom represent months from January through December. The solid pink band shows the maximum (upper edge) and minimum (lower edge) temperature normal for each year and the contained median (middle line) is the average normal for that year (only that information is shown for the years 2003, 2004, and part of 2005). For the years 2005–2009, the added red lines include the daily minimum, mean, and maximum temperatures. The black arrows identify the dates during which trapdoor spider data were collected; the arrows with solid circles identify nights with precipitation (Table 6). The adjacent nights of 21–22 July 2004, 15–16 October 2004, 22–23 October 2004, 23–24 September 2005, 11–12 November 2005, 28–29 September 2007, and 16–17 March 2009 are represented by only 1 arrow.

Soil analysis

I took 3 soil samples, 1 each in the immediate vicinities of burrows 27 (sample 1), 35 (sample 2), and 48 (sample 3) on 2 May 2015. The 3 samples contained, respectively, 13.8%, 20.6%, and 15.0% water, and the #10 sieve results contained gravel particles up to 35, 17, and 27 mm, respectively, in size and were not included in the calculations for sand. All of the soil samples contained small amounts of silt and clay (Table 2). The substrate contains large rocks, under the surface, that were not removed. The second sample contained the most water and the smallest amount of gravel (Table 2).

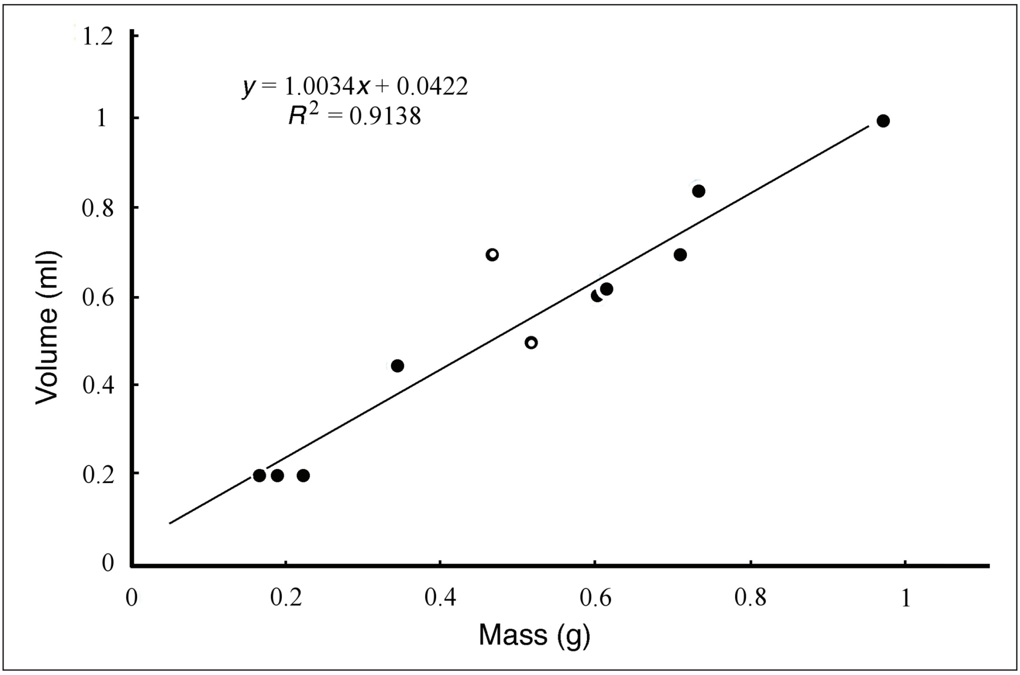

Figure 5. The sizes of 11 preserved specimens of *Myrmekaiphila comstocki* from the study population but not including any spiders from marked burrows. Solid circles represent females, and open circles represent males.

Table 2. Basic analysis of 3 soil samples taken on 2 May 2015 from the immediate vicinities of burrows 27, 35, and 48, respectively. Percent of water = (weight of water) / (weight of dry sample + weight of water). Percent of dry component = (weight of dry component) / (weight of dry sample). Sand = retained fraction from soil sieve numbers 20, 40, 60, 100, and 200; gravel = retained fraction from soil sieve number 10; and silt/clay = retained fraction from soil sieve numbers >200.

		Component of sample							
		Water		Gravel (dry)		Sand (dry)		Silt/clay (dry)	
Sample #	Dry sample (g)	Weight	%	Weight	%	Weight	%	Weight	%
1	80.2	12.8	13.8	43.8	54.6	34.9	43.5	1.5	1.9
2	74.2	19.3	20.6	16.7	22.5	54.5	73.4	3.1	4.2
3	86.3	15.3	15.0	21.3	24.5	64.2	74.8	0.9	1.0

Adjacent microhabitat

Burrows were located closer to bare soil (mean distance = 7.1 cm) than to moss (mean = 22.3 cm), a dicot plant (mean = 36.7 cm), or a grass (monocot plant; mean = 43.6 cm) (Table 3). Soil and moss attached to the top of the trapdoor were not included in the measurements. Leaf litter near the burrow was not removed so as to reduce disturbance in the immediate vicinity of the burrow, and thus might have obscured bare soil or moss that was therefore not measured. Only bare soil and moss, that were clearly visible on the surface were measured.

Camouflage of the trapdoor

The composition of the exterior surface of the trapdoor consisted of tiny bits of soil, small gravel, fragments of dead plant material, or moss (usually green but dry) attached to the silk forming the structure of the trapdoor. The material composing the exterior surface of the trapdoor was extremely similar to that on the ground surface adjacent to the burrow, compared to the surrounding surface of the substrate. The exterior covering of the trapdoor was well camouflaged in the surrounding substrate surface (Fig. 1D–F). The cover materials used more frequently included small bits of bark, fragments of plants (small leaf veins), hyphae, algae, small seeds, soil, pine needles, bits of green grass (uncommon), pine sporangia, small leaves, small twigs, some insect parts, and unidentifiable debris. The covering items were always similar to the surrounding substrate so that nothing about the trapdoor stood out to attract attention; the trapdoor visually disappeared into the surroundings when closed. One exception that I observed was a burrow (Figs. 1A–C) with a trapdoor made of one material (unidentified) that was unlike the surrounding debris and was conspicuous against the normal substrate background.

Direction of open trapdoor

The downward slope of the area west of the trail (Fig. 3) was a ridge at 0° (azimuth) on a ~6° grade above horizontal, and the direction of the west slope of the ridge was at 300°; the area east of the trail faced 0° (azimuth) at a ~3° grade. When open, the direction (azimuth) that the inside surface of the trapdoor usually faced was north or west (Table 4, Fig. 6). Of the 33 open trapdoors measured, only 4 faced up-slope and the other 29 faced down-slope. All of the trapdoors that faced up-slope were in a minor microhabitat situation where the terrain, a few centimeters immediately in front of the open trapdoor, was a down-slope, but the general terrain of the hillside was an up-slope.

Table 3. Distances (cm) from the center of the trapdoor to the nearest visible dicot, monocot, moss, or bare soil (or rock).

	Distance from burrow (cm)		
	Mean	Number of observations	Min–max
Monocot plant	43.6	54	0–130
Dicot plant	36.7	57	1–342
Moss	22.3	65	0–101
Bare soil	7.1	56	0–33

Depth of burrow

Myrmekiaphila comstocki at the study site occupied very rocky soil and, in many cases, the burrows followed rock surfaces, which resulted in a very complex pattern that was 60–330 mm deep (mean = 159 mm; *n* = 28). I did not find plugs or side branches in any of the burrows excavated (none of the burrows excavated were among those marked for this study).

Burrow temperature

The temperature at the bottom of the burrow was 8.5–21.1 °C (mean = 16.2 °C, *n* = 28; Fig. 7). I-button data for the adjacent ground showed a low temperature of -2 °C on 4 March 2007 and a high temperature of 43.5 °C on 12 June 2006 (Table 5; Figs. 7, 8), with a mean of 21.9 °C (Fig. 9). The hourly fluctuations reflect the daily variations and identify short-term weather patterns (Fig. 8A shows all measurements between 22 March and 16 June 2006; notice the consistent patterns between 20 April through part of May). The ground surface, perhaps because of the abundance of larger rocks near the surface, seemed to hold heat better in the late

Table 4. Number and mean azimuth (in °) of open trapdoors of *Myrmekaiphila* facing each of the 4 cardinal directions.

	Quadrant			
	North	East	South	West
n	12	4	5	12
Mean	-13.2	83.8	179.6	289.8

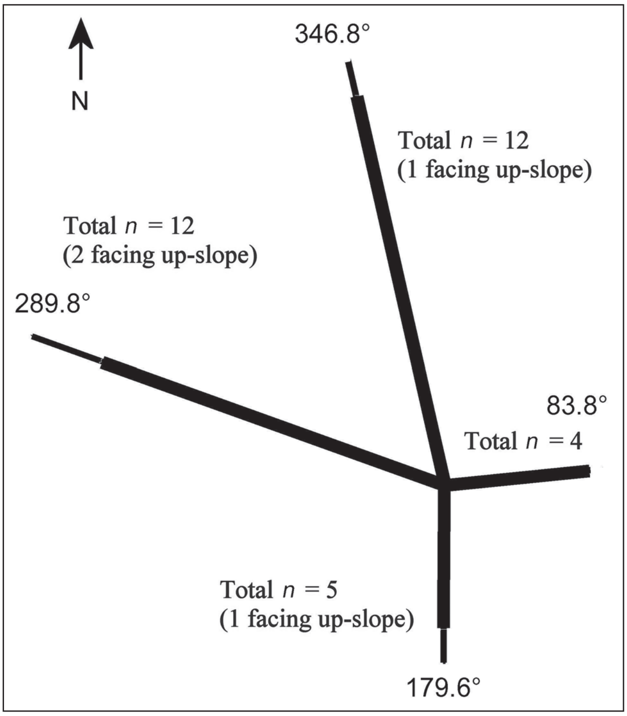

Figure 6. The compass directions (azimuth) of the inner face of open trapdoors of 33 burrows. The azimuth direction of each line is equal to the mean azimuth within the 4 compass quadrates (north quadrate = 315° to 45°, mean = 347°; east quadrate = 45° to 135°, mean = 83°; south quadrate = 135° to 225°, mean = 176°, west quadrate = 225° to 315°, mean = 290°). The total length of each arm is proportional to the total number in that quadrate and the length of the thin portion of the arm is proportional to the number of trapdoors facing up-slope. The arrow marks 0° azimuth.

spring than during early spring; for example, the I-button data showed a relatively sudden change from cooler to warmer temperatures for March through June (Fig. 8A) and then less dramatic change from warmer to cooler temperatures later in the year (Fig. 8B, D). The burrow temperature was positively correlated with the burrow depth (Fig. 10), and the temperature at the bottom of the burrow was never below 7 °C. The burrow temperatures were never close to freezing, and the deeper burrows were warmer than shallower burrows. The air temperature 1 cm above the

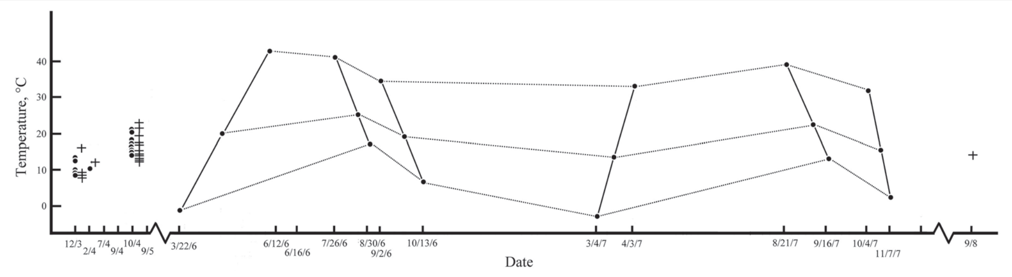

Figure 7. Temperatures at the bottom of the burrows and substrate surface temperatures recorded during this study. At the left side of the figure, the solid circles represent burrow temperatures and the + sign (also one on the right side of the figure) represents the surface temperature of the substrate measured manually. The dates of observation are on the horizontal axis and the 2 breaks separate the burrow and substrate temperatures recorded for individual burrows from the I-Button data of the substrate surface temperature recorded at burrow number 35 during 6 recording sessions from 22 March 2006 through 7 November 2007 (Table 5). The heavier angled lines and their solid circles show the minimum, mean, and maximum temperatures for each I-button recording session; the dotted lines connect the minimal, mean, and maximal temperatures for successive recording sessions.

Table 5. I-Button data on substrate surface temperatures at burrow number 35, which was active during the entire study. The number of observations for 26 Jul–3 Sep 2006 was derived from the sample interval of 60 minutes rather than the 30-minute interval used for all of the other dates. Rate = sample rate per hour. The I-button was covered with a piece of bark to provide shade.

Dates of observations	# of observ.	Mode temp. (°C)	Min temp. (°C)	Date, time of first min.	Max. temp. (°C)	Date, time of first max	# of days	Rate
22 Mar–16 Jun 2006	3034	21.9	-1.39 (2)	24 March, 0439–0639	43.5	12 Jun, 1139	87	60
26 Jul–3 Sep 2006	938	25.7	16.8 (5)	30 Aug, 0711	40.8	3 Aug, 1311	162	60
2 Sep–14 Oct 2006	2329	18.8	7.5	13 Oct, 0223–0753	35.0	10 Sep, 1723	43	30
22 Feb–5 April 2007	8021	9.2	-2.0	4 Mar, 0643, 0743–0813	34.0	3 April, 1343	43	30
17 Aug–28 Sep 2007	8440	22.0	14.0	16 Sep, 0500–0730	42.8	21 Aug, 1300	43	30
28 Sep–10 Nov 2007	7013	9.7	3.5	7 Nov, 0513–0813	31.5	21 Oct, 1313	43	30

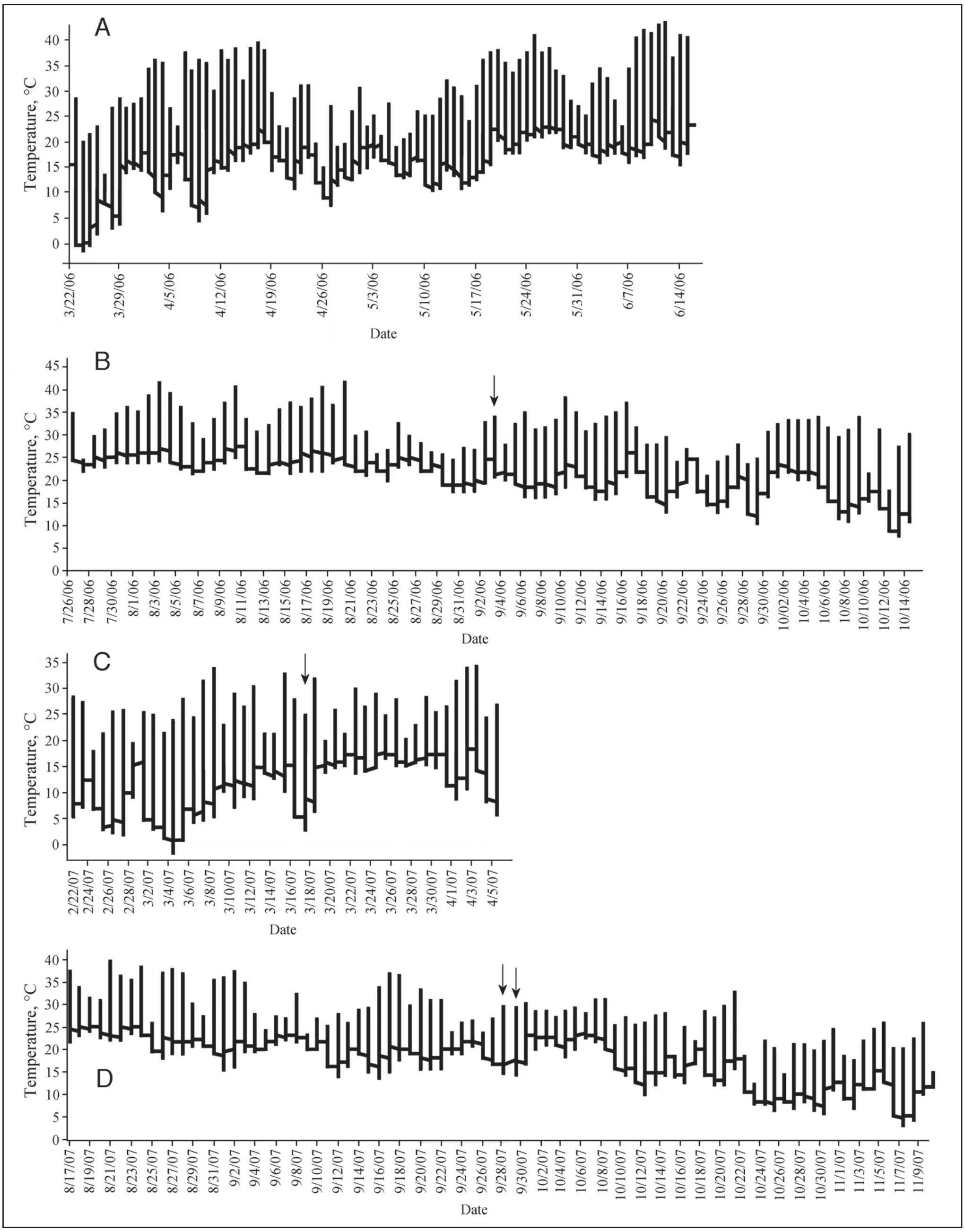

Figure 8. I-button temperatures (°C) recorded from 22 March 2006 through 10 November 2007 at burrow number 35 (*n* = 11,176 measurements). The vertical lines represent the temperature range for a single day; the tops and bottoms of the vertical lines indicate the maximum and minimum temperatures, respectively, for each day. The connecting bars between the vertical lines identify the temperatures of the transition at midnight. The arrows identify nights during which spider data were taken. A = 22 March 2006 through 15 June 2006; B = 26 July 2006 through 14 October 2006; C = 22 February 2007 through 5 April 2007; D = 17 August 2007 through 9 November 2007.

ground surface is the temperature to which a spider would be exposed when the spider is out of its burrow, and that air, if colder, would be the first air mass to sink down the burrow when the trapdoor is open. The ratio of the burrow temperature to the air temperature at 1 cm above the ground surface helps define the difference between the air temperature above the burrow and the temperature at the bottom of the burrow (Fig. 11), with a ratio of 1.0 indicating equilibrium. Only 3 burrow temperatures were cooler than the 1 cm air temperature (Fig. 11), and the coolest

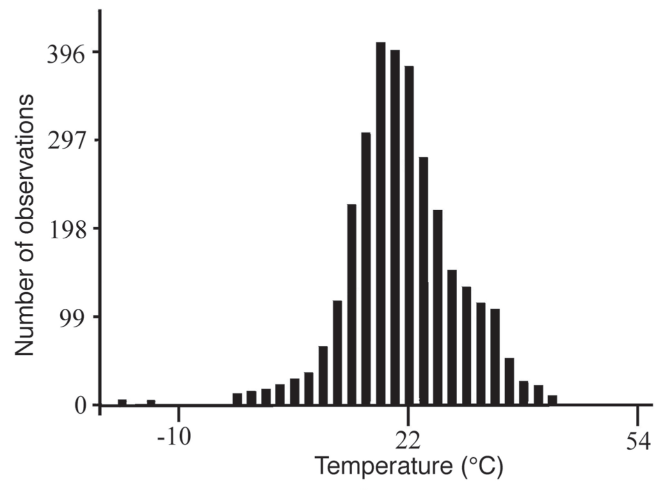

Figure 9. I-button temperatures (C) recorded from 22 March 2006 through 15 June 2006 at burrow number 35 (n = 3043 measurements; mean = 21.9 °C); temperatures were sampled every hour.

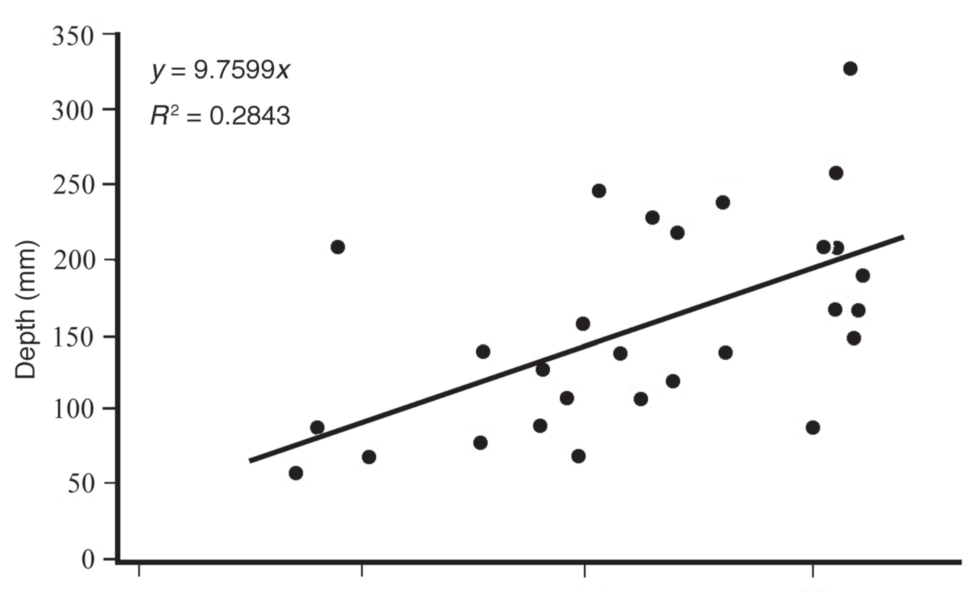

Figure 10. The depth of the burrow compared to the air temperature (°C) at the bottom of the burrow; regression line formula is shown (n = 28). Temperature and depth measurements were made on 3 and 22 December 2003, 28 February 2004, and 15, 16, and 23 October 2004.

was the temperature of the shallowest burrow. The deeper burrows were always warmer than the air temperature 1 cm above the ground surface.

Time that burrows are open

During the study, most of the 688 observations were made between 1900 and 2400 hours (Fig.12) because most of the study time was at night. The trapdoor of a burrow was open 25 percent of the time. Even though heavy rain events occurred

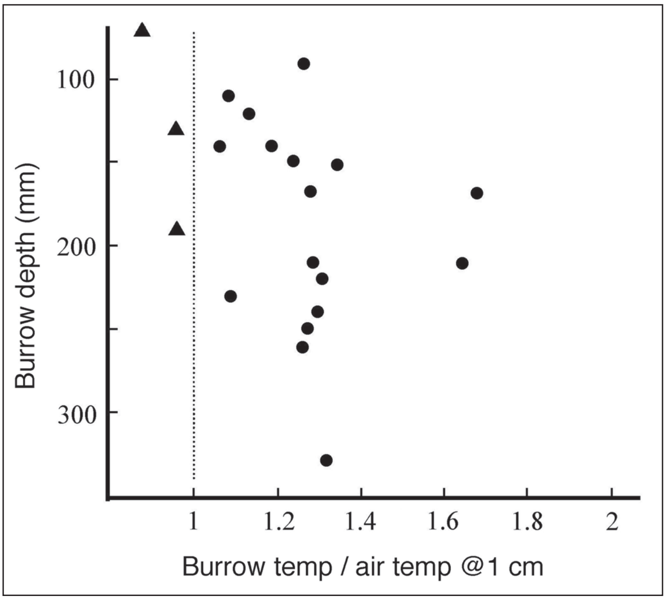

Figure 11. Burrow temperature compared to ambient air temperature (°C) 1 cm above the substrate surface. Triangles indicate burrow temperatures that were cooler than the surface air temperatures, and the circles indicate temperatures warmer than the surface air temperatures. The ordinate axis is the ratio of the burrow temperature divided by the ambient air temperature at 1 cm above the substrate surface; therefore ordinate values less than 1 (to the left of dotted line) identify burrow temperatures cooler than those of the surface air from the burrow temperatures that are warmer.

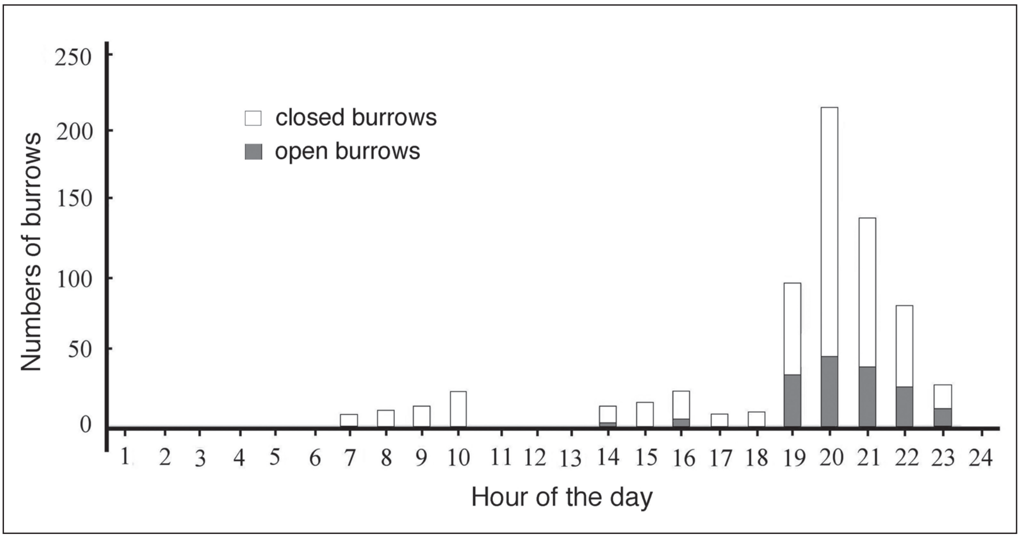

Figure 12. The total numbers of burrows observed during the study compared to the hour of the observation. Unshaded bars represent closed burrows and the gray bars represent open burrows. The ordinate numbers represent the hours of the day (AM to PM).

during the study (Table 6), feeding frequency or other activity of adults or spiderlings was not observed at those times. The best opportunities for observations

Table 6. Dates, times, and precipitation for observations. Before date = amount of precipitation, date of precipitation, number of days prior to observation date; Event date = amount of precipitation on observation date; After date = amount of precipitation, date of precipitation, number of days following observation date. T = trace of precipitation.* indicates observation periods during which spiders were visible at the open trapdoor.

Observation date	Start time	End time	# of observ.	Precipitation (in)		
				Before date	Event date	After date
3 Dec 2003	1940	2035	2	-	0.05	T (4 Dec 2003) 1
22 Dec2003	2030	2040	2	0.24 (15 Dec 2003) 7	0.00	0.55 (23 Dec 2003) 1
22 Jan 2004	1950	-	5	0.20 (18 Jan 2004) 4	0.00	1.40 (26 Jan 2004) 4
28 Feb 2004	2000	-	6	0.18 (25 Feb 2004) 3	0.00	0.63 (1 Mar 2004) 4
30 Apr 2004	2120	2215	8	0.90 (25 Apr 2004) 5	0.00	1.32 (1 May 2004) 6
1 May 2004	2222	2245	9	0.90 (25 Apr 2004) 6	1.32	0.36 (2 May 2004) 1
18 May 2004*	2308	2357	9	0.70 (14 May 2004) 4	0.23	0.7 (24 May 2004) 6
19 May 2004	0800	2236	42	0.70 (14 May 2004) 5	0.00	0.7 (24 May 2004) 5
21 Jul 2004	2104	2153	46	0.56 (9 Jul 2004) 12	0.00	0.14 (24 Jul 2004) 3
22 Jul 2004	2136	2218	50	0.56 (9 Jul 2004) 3	0.00	0.14 (24 Jul 2004) 2
28 Aug 2004	2131	2148	31	0.42 (24 Aug 2004) 4	0.00	0.18 (29 Aug /2004) 1
22 Sep 2004*	2045	2053	25	-	-	-
15 Oct 2004*	1950	2211	46	0.16 (14 Oct 2004) 1	0.00	0.08 (18 Oct 2004) 3
16 Oct 2004*	1924	2039	20	0.16 (14 Oct 2004) 2	0.00	0.08 (18 Oct 2004) 2
22 Oct 2004	2022	2026	3	1.50 (19 Oct 2004) 3	Trace	1.1 (23 Oct 2004) 1
23 Oct 2004*	0755	-	44	T (23 Oct 2004) 0	0.00	1.1 (23 Oct 2004) 0
23 Oct 2004*	1943	2136		T (23 Oct 2004) 0	1.10	0.12 (26 Oct2004) 2
30 Oct 2004*	1447	1715	53	5.00 (28 Oct 2004) 2	0.23	1.03 (31 Oct 2004) 1
5 Nov 2004*	1909	1930	13	0.12 (4 Nov 2004) 1	0.00	0.95 (11 Nov 2004) 6
7 Dec 2004*	1856	1948	39	0.13 (6 Dec 2004) 1	0.67	0.90 (22 Dec 2004) 15
23 Sep 2005	2307	2343	17	0.87 (15 Sep 2005) 8	0.00	5.75 (25 Sep 2004) 2
24 Sep 2005	0900	0937	4	0.87 (15 Sep 2005) 9	0.00	5.75 (25 Sep 2004) 1
11 Nov 2005*	1651	2037	26	0.04 (9 Nov 2005) 2	0.00	5.81 (13 Nov 2005) 2
12 Nov 2005*	0957	1014	37	0.04 (9 Nov 2005) 3	0.00	5.81 (13 Nov 2005) 1
	1954	2020	-	-	-	-
31 Jan 2006*	2006	2026	30	1.99 (1/29/2006) 2	0.00	0.02 (2/2/2006) 3
3 Sep 2006	2019	2042	24	0.06 (29 Aug 2006) 4	0.00	1.13 (12 Sep 2006) 9
17 Mar 2007	2043	2058	5	0.05 (15 Mar 2007) 2	0.00	T (20 Mar 2007) 3
5 Apr 2007*	-	-	-	-	-	-
28 Sep 2007	1950	2031	28	T (27 Sep 2007) 1	0.00	1.53 (2 Oct 2007) 4
29 Sep 2007	2216	2246	28	T (27 Sep 2007) 2	0.00	1.53 (2 Oct 2007) 3
30 Nov 2007	2021	2024	3	0.05 (26 Nov 2007) 4	0.00	0,52 (2 Dec 2007) 2
21 Feb 2008	2008	2011	3	2.68 (17 Feb 2008) 4	0.00	0.31 (22 Feb 2008) 1
10 Apr 2008	2126	2131	3	4.96 (3 Apr 2008) 7	5.07	0.46 (11 Apr 2008) 1
14 Aug 2008	2152	2200	3	0.17 (13 Aug 2008) 11	Trace	0.70 (16 Aug 2008) 4
30 Aug 2008	2228	2234	3	0.01 (29 Aug 2008) 1	Trace	0.48 (2 Sep 2008) 2
29 Sep 2008*	2129	2200	4	T (25 Sep 2008) 4	0.00	0.27 (5 Oct 2008) 6
21 Oct 2008*	2245	2301	4	0.01 (17 Oct 2008) 4	0.00	0.66 (23 Oct 2008) 2
16 Mar 2009	1830	2127	10	0.11 (15 Mar 2009) 1	0.00	T (20 Mar 2009) 4
17 Mar 2009	2030	2106	10	0.11 (15 Mar 2009) 2	0.00	T (20 Mar 2009) 3

during heavy rains were on 1 May 2004 (3.35 cm [1.32 in] of rain), 23 October 2004 (2.79 cm [1.10 in]), and 10 April 2008 (12.88 cm [5.07 in]) (Table 6). Precipitation (rain) was recorded on only 10 of the 35 nights of observation; however, a trace, or more, of rain was recorded from 1 to 12 nights (mean = 3.7 nights) preceding the night of observation and a trace, or more, was recorded from 1 to 15 nights (mean = 3.2 nights) following the night of observation (Table 6). If only the observation periods during which spiders were seen (*n* = 10) at the burrows are considered, then precipitation was recorded 1–4 (mean = 1.8) nights prior to the observation night. However, following the observation night, precipitation was recorded 1–15 (mean = 4.1) nights later, significantly higher (*t* = 0.54, df =18). Even if the 15-day dry period (December 7–22, 2004) following the observation night of December 7 is excluded, the resulting mean of 2.6 nights later is still significantly different (Table 6, *t* = 0.56, df = 19). So, a rain preceding the night of observation is a contributing factor for an individual spider to be active at its trapdoor. Other weather observations (Table 7) show that spiders were visible in the opening of the burrow on clear nights as well as cloudy nights both with and without rain (compare Tables 6 and 7) .

Spider sighting in open burrow entrance

When the trapdoor was open, the spider was present at the entrance in 59% (40 of 68) of the observations. Hinge lengths when spiders were present were 10–25 mm (mean = 17.7 mm, *n* = 40). There was no significant difference in hinge length if the spider was present (*n* = 40) or absent (*n* = 28) at the burrow entrance (*t* = 0.749; df = 66). The resident spider closes the trapdoor from the inside and will even hold the trapdoor closed with its front legs (L.M. Hardy, pers. observ.). It is

Table 7. Additional weather observations in the immediate vicinity of the spider population. Air temp = air temperature at about 1 m above the ground.

Date	Weather observations
19 May 2004	0% overcast; windy
21 Jul 2004	Air temp = 22 °C at 2153 h
22 Jul 2004	Air temp = 24 °C at 2137 h; 22.5 °C at 2203 h; no rain
22 Sep 2004	No wind; air temp = 23.0 °C
22 Oct 2004	Hard rain
23 Oct 2004	Light rain started at 2109 h (during data collection)
30 Oct 2004	Clear
5 Nov 2004	Clear
23 Sep 2005	5.75” rain at night; mist and 24 °C at 2300 h
11 Nov 2005	0% overcast, light wind
12 Nov 2005	Light rain at 1600 h and at 2003–2009 h; moderate rain at 2018 h
31 Jan 2006	Clear, no wind and 11 °C at ca. 2000 h; 9 °C at 2330 h
31 Jan 2006	Windy at 2013 h
5 Apr 2007	No rain, 100% overcast
28 Sep 2007	Clear, no wind
29 Sep 2007	Warm, no wind
10 Sep 2008	100% overcast, slight fog, very light rain earlier
16 Mar 2009	Clear
17 Mar 2009	Clear, slight wind, 0% overcast

not known if the spider ever closes the trapdoor behind it when the spider leaves the burrow temporarily.

Hinge size of the trapdoor

I made a total of 68 hinge length measurements (mean = 17.4 mm, min–max = 5–25 mm) during 643 burrow observations (Fig. 13). Single measurements were made for 19 burrows: 2 measurements each for 11 burrows, 3 measurements each for 5 burrows, and 4 measurements each for 3 burrows (multiple measurements for individual burrows were made on different observation days) (Fig. 14).

Hinge length change

For the burrows with 3 or 4 measurements, 3 decreased and then increased in size, 2 increased and then decreased, 6 only increased, and 2 only decreased in size. The 10 burrows (for which 3 or more hinge measurements were taken) that showed an increase in size over the course of the study had initial sizes of 13–19 mm (Fig. 14, Table 8), and the 3 that decreased in size (Table 8) had initial sizes of 18–20 mm. Three burrows showed decreases from the first to the last measurement of 1 or 2 mm; however, 1 burrow (burrow number 34 with 10 total observation nights; Table 8) showed a 4-mm decrease from 19 (its initial measurement was 18) to 15 mm in 39 days. For all of the trapdoor hinges measured, 15 burrows increased in size (mean increase = 3.3 mm; min–max = 1–8 mm) and 7 burrows decreased in size (mean decrease = 3.7 mm; min–max = 1–11 mm).

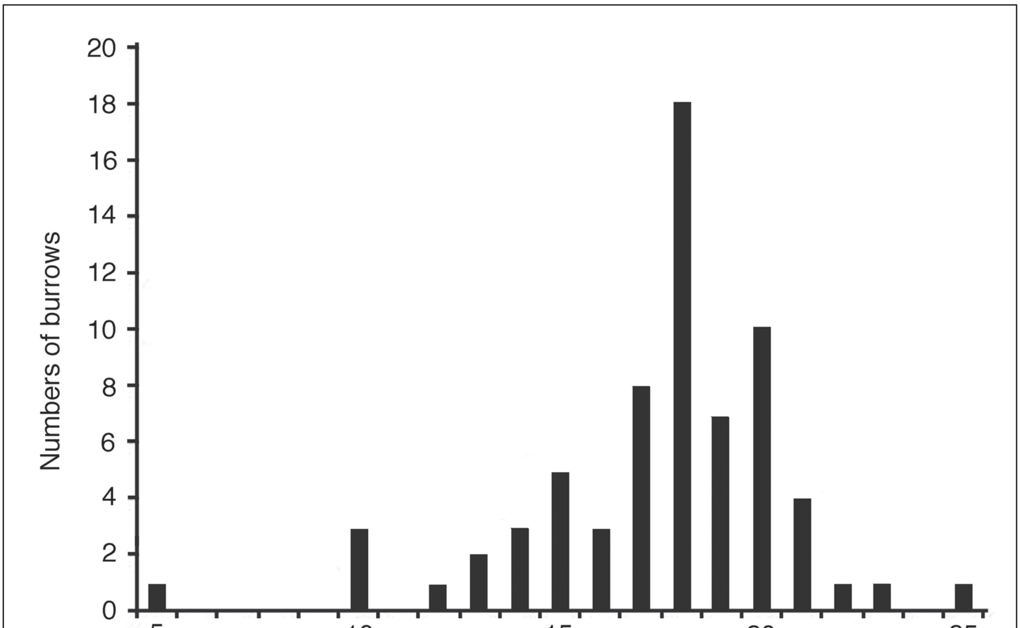

Figure 13. The frequency distribution of burrow trapdoor hinge lengths (n = 68) measured during the study.

Activity season

An indication that a spider was possibly alive and active was the position of the trapdoor in an open (near vertical) position (Fig. 2), and proof that a spider was alive and active was obtained when the spider was observed inside the entrance of the burrow. Over the course of 39 nights of observation, burrows were open on 28 nights and spiders were visible on 19 nights. However, only 20 nights included 10 or more observations, and spiders were seen on 9 of those nights (Fig. 15). There were no open burrows on 5 of those nights, and and no spiders were seen on the ground surface. There were spiders visible inside their burrows on 9 of those nights (Fig. 15). It is possible that study of weather conditions on the nights trap doors are open and spiders are visible vs. the nights when trap doors are closed and spiders are not evident might indentify conditions that are more and less favorable, respectiveley, for *M. comstocki* activity.

Loss of burrows

I compared the trapdoor sizes of burrows to the date of the loss of a spider or its burrow (recorded as the day after the date of the last observation of a live spider in a burrow or of the last observation of an intact open trapdoor of the burrow). I assumed that the destruction or loss of a spider could have occurred any day after the last verification of the spider alive or of an intact open trapdoor. Number of days of observation for each burrow from the beginning of the study to the date of loss was recorded as the day number from the first day of the study,

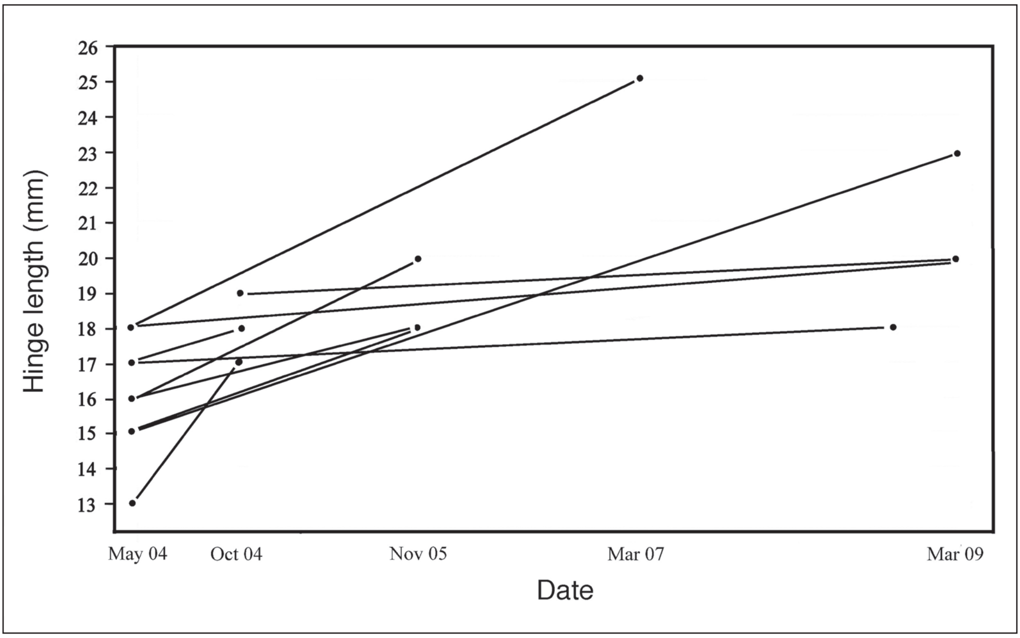

Figure 14. First and last measurements of the length of the burrow trapdoor hinges (mm) of the 10 individual burrows each with 3 or more measurements taken and for which the last measurement was larger than the first. The lines are for ease of viewing the 10 individual burrows only; individual fluctuations of 1–2 mm are not shown.

Table 8. Changes in trapdoor lengths. The burrows that had an increase in size from the earliest to the latest measurement (left columns) and those that decreased in size or stayed the same (right columns).

Burrows that increased in size			Burrows that decreased in size		
Burrow #	Dates	Hinge length (mm)	Burrow #	Dates	Hinge length (mm)
4	28 Feb 2004	14	16	15 Oct 2004	20
4	15 Oct 2004	17	16	23 Oct 2004	20
5	28 Feb 2004	15	16	11 Nov 2005	18
5	15 Oct 2004	18	21	15 Oct 2004	21
6	28 Feb 2004	15	21	30 Oct 2004	20
6	15 Oct 2004	19	26	18 May 2004	19
9	28 Feb 2004	18	26	15 Oct 2004	17
9	15 Oct 2004	21	29	19 May 2004	18
15	15 Oct 2004	19	29	15 Oct 2004	18
15	11 Nov 2005	17	29	11 Nov 2005	17
15	17 Mar 2009	20	29	17 Mar 2007	18
28	18 May 2004	16	34	19 May 2004	18
28	15 Oct 2004	20	34	15 Oct 2004	19
28	23 Oct 2004	19	34	23 Sep 2005	15
28	11 Nov 2005	20	49	19 May 2004	12
30	19 May 2004	13	49	7 Dec 2004	5
30	15 Oct 2004	18	54	19 May 2004	27
30	23 Oct 2004	17	54	23 Oct 2004	16
31	19 May 2004	16			
31	15 Oct 2004	18			
31	23 Oct 2004	19			
31	23 Sep 2005	17			
31	11 Nov 2005	18			
33	19 May 2004	18			
33	15 Oct 2004	18			
33	17 Mar 2007	25			
35	19 May 2004	17			
35	15 Oct 2004	16			
35	17 Mar 2007	18			
35	10 Sep 2008	18			
35	29 Sep 2008	18			
37	19 May 2004	18			
37	28 Sep 2007	21			
37	21 Oct 2008	20			
37	17 Mar 2009	20			
44	19 May 2004	16			
44	23 Oct 2004	20			
46	19 May 2004	15			
46	23 Oct 2004	18			
46	11 Nov 2005	18			
53	28 Sep 2007	15			
53	19 May 2004	15			
53	15 Oct 2004	18			
53	23 Oct 2004	18			
53	17 Mar 2009	23			
56	19 May 2004	17			
56	15 Oct 2004	17			
56	23 Oct 2004	18			

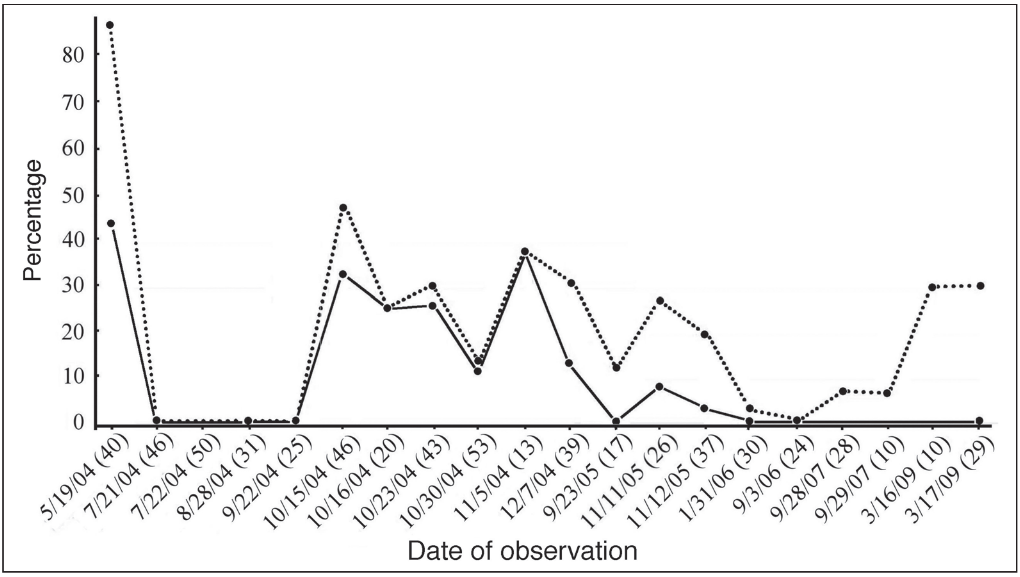

Figure 15. Dates of observation and the percent of spiders visible at the trapdoor (solid line) compared to the percent of burrows with the trapdoor open, but spider not visible, at the time of observation (dotted line). Only dates with 10 or more observations (number of observations given in parentheses) are shown.

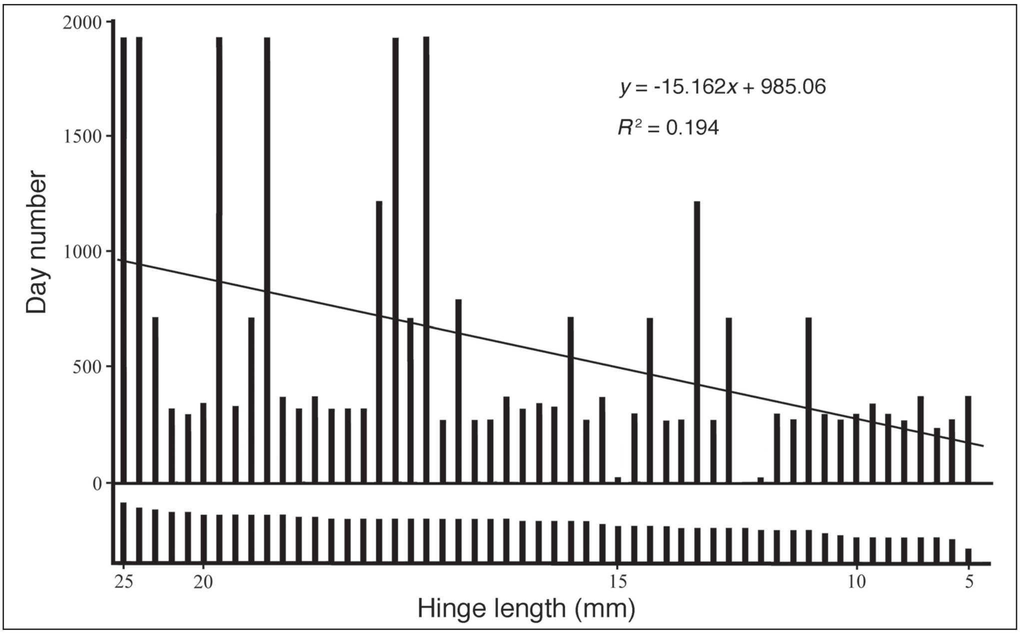

Figure 16. Sizes of 54 burrow trapdoor hinges (length in mm; horizontal axis) compared to the day number (from beginning of study) at the last measurement of the active burrow (vertical axis). The upper vertical bars represent the duration from the beginning of the study (baseline) to the last day of the documented life of the spider in that burrow, in numbers of days since the beginning of the study. The lower vertical bars represent the last measured length of the trapdoor hinge from the largest (25 mm) to the smallest (5 mm).

3 December 2003 (or day 1), to the last day of data collection for that burrow (the last day number of the study was 1932, on 17 March 2009) (Fig. 16). All trapdoors with 2–5 measurements were 5–27 mm in diameter. During the study, some individual burrows were destroyed by a predation event, some natural disaster (for the spider) such as a tree fall that destroyed the burrow, another animal foraging, or another animal digging its own burrow. Those losses of the burrows provide information about survival rates of spiders at different ages. A comparison of the hinge length of a burrow at the last measurement before its destruction and the time interval (in days) from the beginning of the study to the day following the last known date that the spider was confirmed alive or that its burrow was confirmed open and in good condition, suggests that most of the destroyed burrows had hinges that were larger than 15 mm. There were 14 burrows (numbers 15, 16, 27, 29, 33, 35, 36, 37, 45, 46, 47, 50, 52, and 53) that appeared to be undamaged at the end of the study (17 March 2009). The 14 burrows that were still in existence (mean = 17.1 mm, min–max = 11–25 mm) were not significantly different (t = 1.125, df = 52) from the burrows that had been lost (mean = 15.7 mm, min–max = 5–22). When arranged by hinge length compared to the day number of last confirmation of life, the burrows greater than 15 mm in hinge length (mean = 18.9 mm, n = 31; Fig. 17B) had longer survival times (14 burrows for 1932 days; Fig. 17B) than those with lengths of 5–15 mm (mean = 12.1 mm, n = 23); however, a t-test value of 0.005 (df = 52) indicated no significant difference. The timing of burrow loss compared to hinge length shows a positive correlation (Fig. 17). When regression and correlation coefficients are calculated separately for the 2 groups of hinge lengths (≤15 mm vs. >15 mm), the correlation coefficients are different by a magnitude of 10 (Fig. 17A, B), which seems to support the better survival rate of larger burrows. However, the true cause of the apparent correlation is yet to be determined. The rate of loss of the burrows was one burrow per 97 days of observation. At that rate, the remaining burrows could have survived another 3669 days (or until 2019). However, none of the marked burrows were known to be active in April of 2015. Therefore, climatic or environmental changes may have initiated a premature decline of the active burrows.

Population density

The population density was estimated only from the marked burrows studied in this project, which were originally located by being open, visible, and observed at the time of the initial search. Because closed burrows were essentially undetectable visually, this estimate was based only on burrows that were open (and active). The proportion of active and open burrows compared to active but closed at any given time is unknown. Therefore, the estimate obtained here is smaller than the total population of live spiders per hectare. The population density at the study area was estimated at 366 burrows per hectare. However, it appeared that the spider population was more clustered, or at least easier to locate, in some areas than in others. Tiny burrows, 2–4 mm in diameter, were very difficult to find.

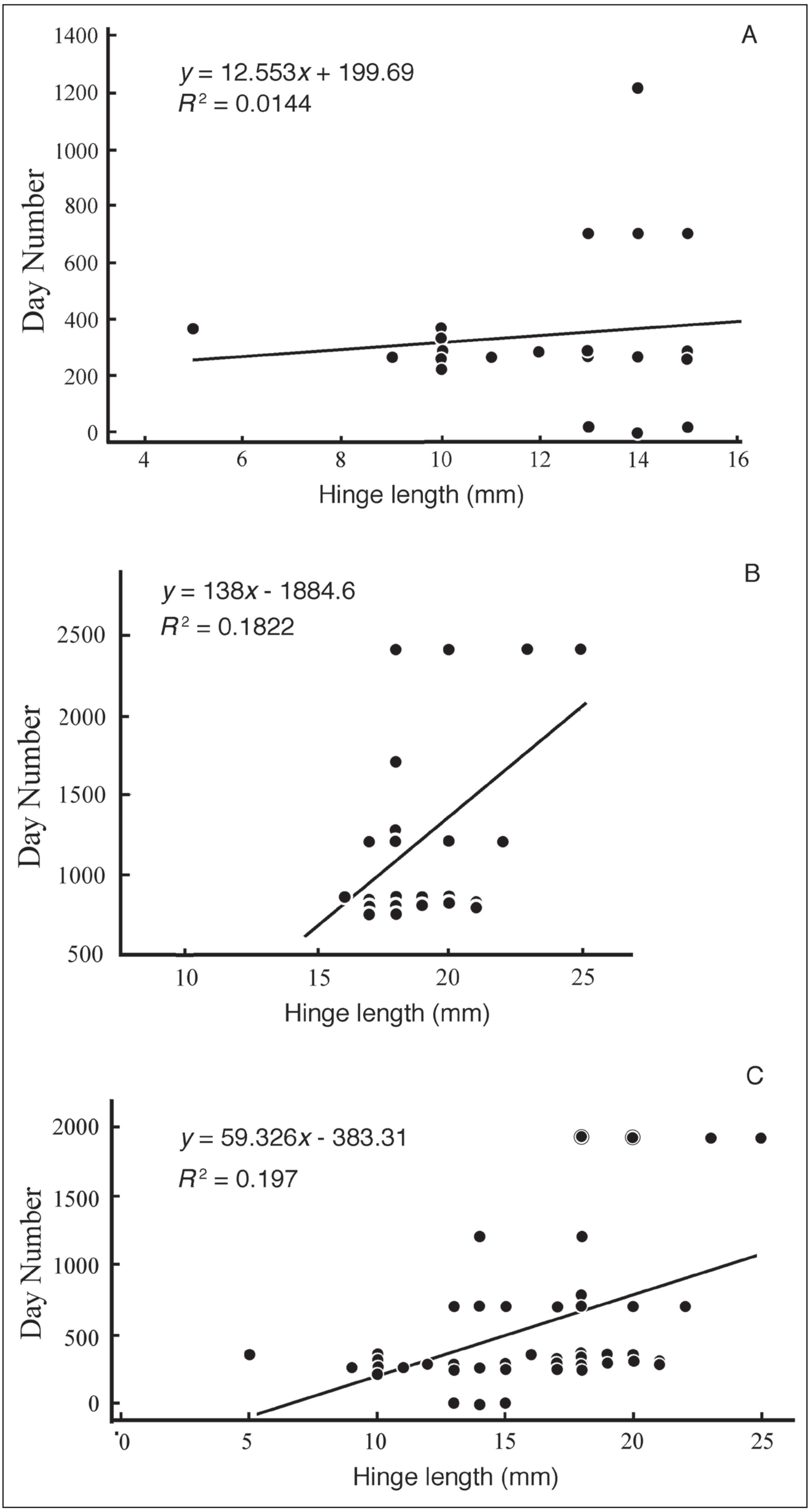

Figure 17. Trapdoor hinge length compared to the day number (from beginning of study) at the last measurement of the active burrow. (A) Burrows with hinge lengths of 5–15 mm, *n* = 23. (B) Burrows with hinge lengths of 16–25 mm, *n* = 31. (C) Each dot represents one, or more, of the 54 burrows measured (several dots represent more than 1 burrow each).

Discussion

Size

Of the 11 specimens measured during this study (Fig. 5), the 3 smallest were immature females; the remaining 8 were sexually mature. The 2 mature males were captured on the surface, and had emaciated abdomens, but each had the legs and cephalothorax as large as the largest adult females. Sexual maturity in females in this study was reached at a mass of ~0.4 g and a volume of ~0.4 ml. These specimens were captured in spring and fall, mostly at night (Table 9).

Soil analysis

The rocky soil used by *M. comstockii* in this study is probably similar to the loose and rocky soil reported by Atkinson (1886b) for *M. foliata* in North Carolina. Burrows of *M. comstockii* are common in other areas of the OMBS, including some of the roads and trails in lowland areas that likely contain more sandy soil, such as that reported by Hunt (1976) for *Myrmekiaphila* in Georgia. Bond et al. (2012b) reported mixed deciduous/pine forest at the type locality for *M. tigris* in Alabama, but provided no details about soil structure.

Adjacent microhabitat

The understory in the vicinity of this population is typical of the second-growth mixed deciduous/coniferous forest of the OMBS (MacRoberts et al. 2005). An open canopy and sparse understory coverage might be important for *M. comstockii* in this area.

Camouflage of the trapdoor

Particles used to cover the trapdoor, which camouflages the door to the detection of other animals or provides insulation, are almost always materials also found within a short distance (a few cm) from the trapdoor. The camouflaging properties might include a variety of spectral frequencies (visible, infrared, or ultraviolet) to guard against predators using visual cue as well as possibly olfaction cues emanating from the interior of the burrow. The materials covering the trapdoors may also insulate against temperature extremes.

Direction of open trapdoor

Alignment of the trapdoor, which was always facing down-slope in regards to the immediate ground in front of the door, might be an adaptation to reduce the possibility of water flowing downhill and into the open burrow during rain events. This finding suggests the ability to detect subtle differences in the slope of the terrain in the immediate vicinity of the burrow. Based on the few observations recorded here (Fig. 6), the distance of slope detection might be limited to only a few cm.

Effect of litter over burrow (vegetation)

Most of the burrows were in the open and not closely associated with vegetation (Table 2). The most frequent (not measured) obstruction for the burrows was the presence of fallen leaves over the burrow site and, occasionally, raising a leaf

Table 9. Capture details for 11 specimens of *M. comstocki* from the vicinity of the study population. Field numbers are all LMH.

Museum number	Field number	Sex	Weight (g)	Volume (ml)	Collection date	Mature?	Notes
370	13869	F	0.972	1.00	21 Oct 2008	Yes	In horizontal burrow in creek bank between upper and middle ponds, 1830–2100 h
371	13870	F	0.339	0.45	21 Oct 2008	Yes	In horizontal burrow in creek bank between upper and middle ponds, 1830–2100 h
372	13871	F	0.186	0.20	21 Oct 2008	No	In horizontal burrow in creek bank between upper and middle ponds, 1830–2100 h
373	13872	F	0.167	0.20	21 Oct 2008	No	In horizontal burrow in creek bank between upper and middle ponds, 1830–2100 h
1840	12426	F	0.601	0.60	7 Apr 2001	Yes	On forest leaf litter, 2035 h, 1.3 m south of trapdoor
1841	12434	F	0.709	0.70	22 May 2001	Yes	Dug our while trenching for electric line
1866	12479	M	0.467	0.70	11 Nov 2001	Yes	Between wall and foundation of building; starving
1900	12524	F	0.222	0.20	8 May 2002	No	Dug out of burrow at night
1908	12532	F	0.605	0.60	8 May 2002	Yes	-
2253	13092	M	0.517	0.50	14 Oct 2005	Yes	Starving
2333	13224	F	0.732	0.85	12 Nov 2005	Yes	-

would reveal the active and open burrow. Such burrows, even covered by a leaf, probably were not impacted negatively by the leaf, and the covering leaf might have had a positive impact by providing an avenue for potential prey that would be moving under the leaf litter. Leaf litter covering a burrow might have influenced the size and quality of prey passing near the burrow opening. Larger prey crossing on top of the leaf litter, rather than going under the leaves, would be less available to mature spiders. However, smaller prey moving under the leaves would be available to smaller spiders. Therefore, the extent of leaf litter might select for smaller (younger) spiders by providing for more appropriate-sized prey moving between the ground surface and the leaf litter and against larger spiders because larger prey might be more abundant near the top of the leaf litter, out of reach of trapdoor spiders located under the litter. Also, a covering of leaf litter might modify the temperature and humidity of the microenvironment, thereby broadening (or changing) the environmental tolerance of the spider population.

Predation

Myrmekiaphila comstockii is considered to be usually nocturnal; however, males often wander on the surface during daylight, and females hunt from their open trapdoors at all hours. Spiders as large as *Myrmekiaphila* could serve as prey for large centipedes and possibly a few insects. The larger terrestrial frogs, lizards, turtles, and snakes would probably eat wandering *Myrmekiaphila. Megascops asio* (L.) (Eastern Screech-Owl) takes invertebrates and is a crepuscular/nocturnal hunter (Alsop 2001); however, most passerine birds that eat spiders are diurnal and appear to specialize on non-burrowing spiders (Gunnarsson 2008). Mammals that might be the more important predators of *Myrmekiaphila* include *Blarina brevicauda* (Say) (Northern Short-tailed Shrew), *Cryptotis parva* (Say) (Least Shrew), *Sorex longirostris* Bachman (Southeastern Shrew), *Scalopus aquaticus* (L.) (Eastern Mole), several species of rodents, *Didelphis virginiana* Kerr (Virginia Opossum), *Procyon lotor* (L.) (Raccoon), *Mustela vison* Schreber (Mink), *Mephitis mephitis* (Schreber) (Striped Skunk), *Spilogale putorius* (L.) (Eastern Spotted Skunk), *Canis latrans* Say (Coyote), *Lynx rufus* (Schreber) (Bobcat), *Urocyon cinereoargenteus* (Schreber) (Gray Fox), *Vulpes vulpes* (L.) (Red Fox), and *Ursus amercanus* Pallas (Black Bear).

The open trapdoor of *Myrmekiaphila* is highly visible in both day and night and could serve as an invitation to an appropriate predator; however, the depth (up to 33 cm) of the burrow would protect the spider from most predation attempts. I have never seen evidence of a predator's attempts to dig up a burrow to a depth of more than ~4–5 cm deep. When closed, a burrow is almost invisible (due to camouflage material stuck to the outside of the trapdoor) on the ground surface in day or night, but might be detectable by an olfactory signature.

Burrow direction

The position of the trapdoor so that the hinge is on the up-slope side of the burrow, which, in addition to the sealing effect of the silk lining, would protect the burrow from water flowing over the surface, (Hutchinson 1904). If the hinge is on the down-slope side of the burrow, then the open trapdoor could funnel water into the burrow. Close examination of the 4 burrows that had the hinge on the down-slope side of the burrow revealed a slight depression on the up-slope side of and adjacent to the burrow. It is conceivable that the spider interpreted that slight depression as the down-slope side and, therefore, had constructed the trapdoor on the wrong side of the burrow. If water flowing into the burrow is a negative selective event, and such a trait was genetically based, then the tendency to construct the burrow hinge on the wrong side would be selected against, thereby strengthening the genetic tendency to explore or detect the slope of the terrain farther from the trapdoor, thus avoiding the microhabitat irregularities immediately adjacent to the trapdoor.

Depth of burrow

The burrows of the population of *M. comstocki* reported herein were much deeper than those reported for *Aliatypus* by Coyle and Icenogel (1994). The greater depth of burrows in this population could be influenced by the extreme weather conditions during the year, the rocky composition of the soil, or the predator populations.

Burrow temperature

The burrows provide a retreat that can protect the spider from extreme environmental temperatures. The temperature at the bottom of the burrow was positively correlated with the depth of the burrow below the ground surface (Fig. 13) and is probably an important factor in the long-term survival of individuals if spiders continue to deepen their burrows as they increase in age and size. A comparison of burrow temperatures with the air temperature 1 cm above the substrate surface (Fig. 11) shows the increase in warmth of the burrow at greater depths. Only 3 burrows had temperatures that were cooler than the air temperature at 1 cm above ground (solid triangles in Fig. 11), and 1 of those was the shallowest of the burrows studied. At least 2 factors could account for the cooler temperatures of those 3 burrows: (1) the burrows might have been in contact with large rocks that might influence the burrow temperature, (2) the burrows might have been recently enough opened that the entering outside air had not yet equilibrated to the warmth of the deeper burrow walls.

Time that burrows are open

Trapdoors were open at different times during the day, apparently uncorrelated with cloud cover, although heavy rain seemed to reduce the presence of a spider at the open trapdoor. The purposes of the spider being at the open trapdoor could include lying in wait for food, testing weather conditions, letting outside air into the burrow chamber, or advertising for a mate.

Spider sighting in open burrow entrance

When the trapdoor was open, the resident spider was at the entrance most (59%) of the time, but there did not seem to be a relationship between status of the door as open and the size of the trapdoor hinge. Also, an open trapdoor, without a spider visible, was not an absolute indication that the spider was not in attendance; the resident spider could have been just out-of-sight in the burrow or may have just retreated at the approach of the observer.

Pattern of activity

Spider burrow number 16 was open on 20 October 2006, when only 4 others were open during a cool night, but number 16 was closed on the next night (21 October, a much warmer night) when 10 others were open. If a spider is successful in catching prey on one night, then it might not need to hunt (open the trapdoor) during the next night, even though the hunting conditions appear to be better. Engelbrecht (2013) found that activity of 4 species of the genus *Ancylotrypa* (Cyrtaucheniidae) in South Africa could be predicted by soil moisture and that those species were more active following heavy rainfall. Rain did not fall on most observation nights for this study, and there was no correlation between rainfall preceding versus following the observation night. However, when spiders were present at the trapdoor of the burrow there was a significant correlation, so that the time preceding the night of observation was shorter that the time interval for rain following the night of observation.

Open frequency of burrows

Costa and Conti (2013) found that adults of an undescribed, burrowing species of *Ariadna* (Segestriidae, not a mygalomorph) in the Namib desert of Namibia closed their burrows for longer periods of time following exceptionally heavy rain events, but spiderlings opened their burrows shortly after a rain event. Such results suggest that the spiderlings, which must feed frequently, responded quickly to the rain event as a trophic resource due to increased availability of small prey items as a result of the available water. The heaviest rain during this project (12.88 cm [5.07 in] on 10 April 2008), preceded by one of 12.60 cm (4.96 in) 7 days earlier, was followed by 1.17 cm (0.46 in) 1 night later (Table 6); however, only 2 burrows were open (of trapdoor lengths of 20 and 23 mm). The next largest rain (3.35 cm [1.32 in]) occurred on 1 May 2004 and was preceded by 2.29 cm (0.90 in) 6 nights before and followed by 0.91 cm (0.36 in) the next night (Table 6); trapdoor lengths of the 7 burrows observed during that rain were 10, 10, 18, 19, 20, 20, and 22 mm (3 were closed and 4 were open).

Hinge size of the trapdoor

The trapdoor length can probably be used to estimate the relative size of both the burrow diameter and the size of the spider. The rate of change of the hinge length can be used as an indicator of the relative change in burrow diameter and, possibly, the size of the spider. Does a pregnant female reduce the diameter of her trapdoor after oviposition when she is smaller? Also, can changes in burrow diameter reflect the effects of weather and seasonal changes? Changes of only 1 or 2 mm per year can be attributed to measurement error or changes in soil moisture or weather conditions. Trapdoor hinge lengths that increased could have been the result of the resident spider modifying the burrow and trapdoor as the spider increased in size and age. Two burrows (numbers 49 and 54) had unusual decreases in size of 7 to 13 mm, respectively, within 5 to 7 months (Table 7). These 2 burrows were active, and the change in burrow diameter suggested that the original resident spider was gone and a much smaller spider had occupied and modified the burrow. Direct evidence for these changes is lacking because the individual spiders were not marked for individual recognition. However, in each case of hinge length reduction, there was no evidence that the burrow and trapdoor was damaged between the observation visits that recorded a change in size.

This study focused on the ecology of adult-sized spiders and their burrows; however, during data collection, tiny burrows (~2–5 mm wide) were frequently observed within a few cm of marked adult-sized burrows. Bond and Coyle (1995) found only 9 small burrows in the immediate vicinity of large (20–23 mm) burrows and suggested that the lack of small burrows supports a hypothesis that the primary dispersal mode for that species is ballooning of spiderlings away from the burrow in which they hatched. Therefore, my data suggests that ballooning of spiderlings is not the primary dispersal mode for *Myrmekiaphia comstocki* in this microhabitat. In an extensive study of ballooning in Switzerland, Blandenier et al. (2013) reported 26 species that used ballooning for dispersal; however, none were mygalomorphs even though 3 subspecies of mygalomorphs (Atypidae) are known from Switzerland.

Activity season

Summer and early autumn (July through September) seemed to be the seasons that had fewer trapdoors open and spiders visible at the entrance (Fig. 15). This finding might be related to temperatures, rainfall, and/or a reduction of prey availability.

Loss of burrows

Burrows with larger trapdoor lengths were lost more frequently than smaller trapdoor sizes (Figs. 16, 17). These larger burrows had been occupied for a longer period of time so that habitat changes would have a greater impact on the individual spider's behavior and habits; whereas, smaller burrows might not have been occupied long enough to be negatively impacted by the habitat change and they might not be as vulnerable to foraging predators. Larger trapdoors are easier to locate visually that smaller ones. Loss of burrows might also be related to increasing canopy cover of the maturing forest and the increase in leaf litter on the forest floor. The death of an older (larger) spider probably results in the loss of the trapdoor or burrow due to lack of repair or defense.

Population density

Applying the average weight (0.5036 g) of the female spiders in the preserved sample to our estimated population density of 366 burrows per hectare would result in a female biomass of 0.184 kg/ha. If the sex ratio is 1:1, then the equal population of males would result in a total biomass of *Myrmekiaphia comstocki* at about 0.368 kg/ha. The density of burrows (0.0366/m^2) is far smaller than that estimated for *M. torreya* in Florida by Gertsch and Wallace (1936).

Comparison with *Aliatypus*

One of the more comprehensive studies of trapdoor spider ecology was that of Coyle and Icenogel (1994), who studied all of the species of *Aliatypus* in western North America. That genus is the only one in the family Antrodiaetidae that makes trapdoors and is not closely related to *Myrmekiaphila* (Cyrtocthinidae). Even though the *Myrmekiaphila* burrows in my study area were on north-facing slopes, the maximum slope of 6° is considerably lower than the minimum of 45° that they recorded for *Aliatypus*. Also, the *Myrmekiaphila* burrows were much deeper (up to 330 mm) and in a less arid area than *Aliatypus* at 51 mm in the driest desert studied by Coyle and Icenogel (1994). I never saw any digging activity from the *Myrmekiaphila* nor any freshly excavated soil pellets near the entrances, and none of the entrances showed the tabs recorded by Coyle and Icenogel (1994).

Adaptations for environmental tolerance

Specialized ecological requirements for a species would narrow that species' tolerance for fluctuations of abiotic factors in a changing environment. Fluctuations of abiotic environmental factors could provide selective pressure for other species with more generalized environmental requirements within a local community. A balance of specialized versus generalized sets of parameters would allow continual survival (success) of a population and contribute to the success of that species. Characters that might promote specialization in burrow structure include the rocky composition of the soil, the composition of the surrounding vegetation, and climatic conditions (all abiotic factors), and the composition of the predator community (a biotic factor). Characters that support generalization of environmental tolerance include tolerance to variable climatic conditions, generalized diet requirements, and morphological characters adapted to variations in local soil structure.

Questions for future study

How often and why do individual female spiders move to another, pre-existing burrow, or dig a new burrow? Do young *M. comstocki* balloon, and if so, under what conditions? What species are more frequently taken as prey by *M. comstocki*, and which species are known predators on *M. comstocki* (both groups are poorly known)? What is the behavior of *M. comstocki* during heavy rain (if, and when, do they open the trapdoor to hunt)? What factor(s) trigger a spider to open the trapdoor? Is there a predictable microhabitat in which this species prefers to locate its burrow? In this environment of the Ouachita Mountains, the microhabitat that might predict the presence of *M. comstocki* would include slightly sloping terrain, probably less than 10° angle from horizontal, little vegetational ground cover, and light leaf litter. Do they move burrow locations? Do surface-active diurnal males and secretive burrow-restricted females face significantly different selection pressures due to the different foraging habits of predators?

Summary: Key Findings

1. Nine females were larger (mass: mean = 0.50, min–max = 0.17–0.97 g; volume: mean = 0.53, min–max = 0.20–1.0 ml) than 2 males (mass = 0.47, 0.52; volume = 0.70, 0.50 ml).
2. Three soil samples contained, respectively, 14.5, 23.3, and 14.0% water; gravel up to 17 mm in size; 43.5, 73.4, and 74.8% sand; and 1.9, 4.2, and 1.0% silt/clay.
3. The burrows were closer to bare soil than to moss or a dicotyledonous plant and farthest from a monocot. Leaf litter was usually present.
4. The exterior surface of the trapdoor was covered with tiny bits of soil, small gravel, fragments of dead plant material, or green moss attached to the silk surface of the trapdoor.
5. The trapdoors were usually hinged on the uphill side, and most were facing north to northwest following the slope of the terrain. The immediate study area was on a slope of 3–6° above horizontal.
6. Burrows were 60–330 mm deep in very rocky soil.
7. Temperatures at the bottoms of the burrows were never below freezing and were usually warmer than winter surface temperatures and cooler than summer surface temperatures.
8. The trapdoors were open 25% of the time and were open more often following a rain event.
9. Loss of burrows (destroyed by predators or climatic factors) was not related to hinge length.
10. The population density of the study population was estimated at 366 burrows per hectare.

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