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Author: Carrel, James E.

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Differential survival of *Geolycosa xera archboldi* and *G. hubbelli* (Araneae, Lycosidae) after fire in Florida scrub

James E. Carrel¹: Division of Biological Sciences, 209 Tucker Hall, University of Missouri-Columbia, Columbia, Missouri 65211-7400, USA. E-mail: carrelj@missouri.edu

Abstract. A replicated pre- and post-burn study of survival of small and large *Geolycosa xera archboldi* McCrone 1963 and *G. hubbelli* Wallace 1942 in Florida scrub was conducted. These two syntopic species were chosen because *G. x. archboldi* prefers large gaps of barren sand in the scrub matrix, sites with little fuel for fires, whereas *G. hubbelli* strongly favors small gaps having some leaf litter, sites with modest or high fuel-loads. On the basis of these species-specific differences in microsite characteristics, I hypothesized that *G. x. archboldi* would be very fire tolerant but that *G. hubbelli* would be fire intolerant. I established two size classes for the *Geolycosa*: small spiders had 3–5 mm diameter \times 5–9 cm deep burrows; large spiders had > 6 mm diameter \times 10–17 cm deep burrows. Burrows of 25 spiders in each species \times size class were marked before a burn in seven burn units (= fire management areas) and survival or mortality of each occupant was ascertained over the course of 5 days post-burn. Thus, the experimental design was 2 species \times 2 size classes \times 7 burn units \times 25 replicates/burn unit ($n = 700$ spiders total). Survivorship was very high in small and large *G. x. archboldi* and in large *G. hubbelli* (93–96%), but it was low in small *G. hubbelli* (35%). Temperature recordings suggest mortality in small *G. hubbelli* was caused by high temperatures at depths of 5–10 cm during intense, but brief burns that characterize fires in Florida scrub. In contrast, large *G. hubbelli* had burrows sufficiently deep so that most of them did not experience lethal temperatures during burns.

Keywords: Burrowing wolf spiders, endemism, Lake Wales Ridge, body size, fire ecology

Florida scrub is a fire-prone ecosystem confined to ancient sand ridges in the peninsular part of the state. This ecosystem also supports biotic communities that comprise a globally important, imperiled center of endemism (Deyrup 1989; Deyrup & Eisner 1993; Dobson et al. 1997; Menges 1999; Marshall et al. 2000; Estill & Cruzan 2001; Weekley et al. 2008). Presumably, as part of the suite of characters needed to survive in scrub, endemic species have evolved adaptations to frequent landscape-level burns that rapidly consume the leaf litter and standing vegetation. For example, the dominant woody shrubs have most of their biomass below ground, so they survive and quickly regenerate the shrub matrix by sprouting. In contrast, most endemic herbs are killed by fire and post-burn increases in abundance are due to seedling recruitment (Weekley & Menges 2003, and references therein). Scrub animals have three common methods for coping with fire at a landscape scale. On the one hand, some such as sand skinks (*Plestiodon reynoldsi*), gopher tortoises (*Gopherus polyphemus*), and flightless pygmy mole crickets (*Neotridactylus archboldi*), persist in place by exploiting a subterranean life style in the sandy soils (Robbins & Myers 1992; Deyrup 2005). On the other hand, the Florida scrub jay (*Aphelocoma coerulescens*) and other highly dispersive animals flee the oncoming flames on wing or foot and settle in unburned scrub (Robbins & Myers 1992). A third approach, one used by weak-flying insects and arboreal spiders, such as the red widow spider (*Latrodectus bishopi* Kaston 1938), is to experience high mortality during a burn and to recolonize subsequently from nearby, unburned refugia (Deyrup & Eisner 1996; Carrel 2001, 2008).

Two species of rare burrowing wolf spiders, *Geolycosa xera archboldi* McCrone 1963 and *G. hubbelli* Wallace 1942, are

endemic to oak scrub on the Lake Wales Ridge in the middle of peninsular Florida (Marshall et al. 2000). Because the spiders spend most of their lives below ground in tubular burrows they construct in the sand, I expected that they might be fire tolerant, similar to other subterranean animals. But knowing that small individuals build much shallower burrows than larger, older individuals (Table 1 and Figure 1), I hypothesized that survival of a burn in *Geolycosa* might be size dependent because smaller spiders build more shallow burrows than larger spiders and, as a result, small spiders could be more exposed to lethal temperatures that penetrate the upper layer of soil when scrub is burned. In addition, because *G. x. archboldi* prefers large ($> 1 \text{ m}^2$), barren gaps of sand and does not decorate its burrow entrance with a turret, whereas *G. hubbelli* favors small gaps ($\sim 0.1 \text{ m}^2$) in the shrubby matrix having leaf litter from which it obligatorily builds a turret (Carrel 2003a, b), I also hypothesized that the latter species might be more likely to perish in a fire. To test these ideas, I conducted a pre- and post-fire study of survival (or mortality) of individual *G. x. archboldi* and *G. hubbelli* in two size classes (small and large individuals, Tables 1 and 2) over the course of several burn events in Florida scrub. I also collected ambient temperature data in *Geolycosa* burrows and on the soil surface during a fire. To my knowledge this is the first replicated, quantitative study of survivorship in any spider exposed to burning of its habitat, and it may be one of the few such studies with any terrestrial arthropod to date (Warren et al. 1987; Whelan 1995; Siemann et al. 1997; Swengel 2001).

METHODS

Study site.—I conducted a pre- and post-fire study of *Geolycosa* survival in flat, oak scrub at the 2101 ha Archbold Biological Station, in southern Highlands County, Florida (elev. 36–46 m, 27°11'N, 81°21'W). The work was performed in the most extensive vegetative association, called scrubby

¹Current address: Archbold Biological Station, 123 Main Drive, Venus, Florida 33960, USA.

Table 1.—Depth and volume of burrows constructed by small and large *Geolycosa* spiders. Typical data were calculated using best-fit regression equations published by Carrel (2003a).

Spider species	Burrow properties	Burrow size class (diameter, mm)	
		Small (3–5)	Large (6–15)
<i>G. xera archboldi</i>	Depth (cm)	4.6–8.2	10.0–15.4
	Volume (cc)	0.4–2.3	4.5–19.7
<i>G. hubbelli</i>	Depth (cm)	5.6–9.1	10.3–16.6
	Volume (cc)	0.7–2.8	4.5–49.0

flatwoods, which has fire-resistant slash pines (*Pinus elliotii*) scattered in a dense matrix dominated by low-growing shrubby oaks (*Quercus inopina*, *Q. chapmanii*, and *Q. geminata*), palmettos (*Serenia repens* and *Sabal etonia*, *Arecaceae*), and shrubby lyonias (*Lyonia ferruginea*, *L. fruticosa*, and *L. lucida*, *Ericaceae*) (Abrahamson et al. 1984). For management purposes, the scrub at Archbold is organized into a series of 187 burn units and a detailed history of burning in each unit is available (Main & Menges 1997; unpublished Archbold records). I was able to work in seven units, ranging in size from 4.6 to 66.5 ha, two of which were burned in February 2001, one in October 2002, two in July 2007, and two in August 2007. Voucher specimens of both *Geolycosa* species were deposited in the Invertebrate Collection at Archbold.

Experimental design.—I haphazardly located 25 small (3–5 mm diam.) and 25 large (6–15 mm diam.) burrows of both

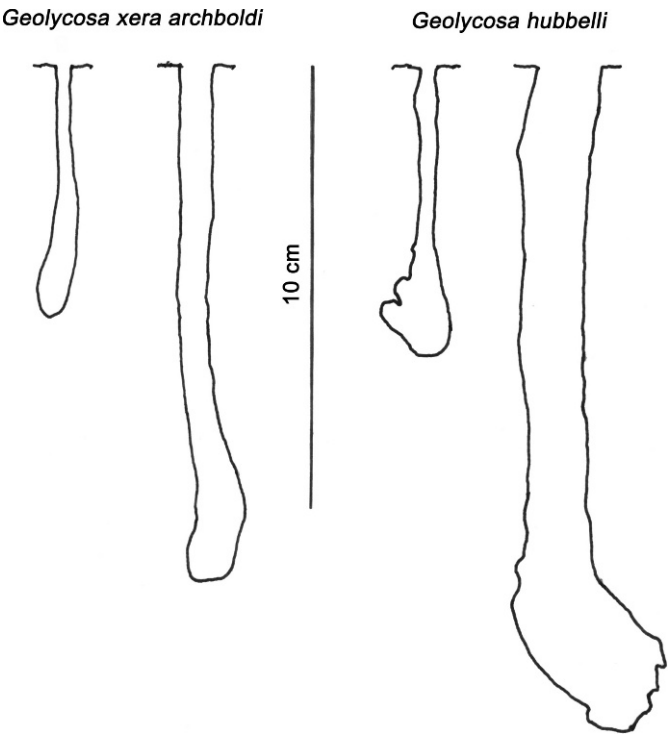


Figure 1.—Silhouettes of small and large burrows of *Geolycosa xera archboldi* and *G. hubbelli* prepared from representative plaster casts (Carrel 2003a). Note interspecific difference in the architecture of burrow bases.

Table 2.—Attributes of two *Geolycosa* species placed into two size classes (small and large) based on diameter of their burrow openings, for study of survivorship after fire. Typical data were calculated using best-fit regression equations (Carrel 2003a). Sample size in this study (*n*) for each species \times size class is also given.

Spider size class		<i>G. x. archboldi</i> (turret absent)	<i>G. hubbelli</i> (turret present)
Small	Burrow diameter (mm)	3–5	3–5
	Carapace width (mm)	1.4–2.3	1.5–2.1
	Body mass (mg)	8–30	8–17
	Sample size (<i>n</i>)	175	175
Large	Burrow diameter (mm)	6–10	6–15
	Carapace width (mm)	2.7–4.3	2.4–5.1
	Body mass (mg)	40–230	25–600
	Sample size (<i>n</i>)	175	175

Geolycosa species by visually searching in seven different burn units 1–2 days before each was burned. Burrows were > 10 m from the perimeter of a burn unit to avoid edge effects, particularly kerosene-induced flames from drip torches used to ignite the leaf litter and vegetation. In previous studies (Carrel 2003a) I showed that the persistently open, circular burrows render these spiders very detectable: by conducting a rapid, but thorough visual search of an area (10–100 m²), one typically locates 90–95% of individuals actually present. Furthermore, the presence or absence of a turret constructed from leaves and debris, held in place with silk around the burrow opening, is a reliable tool for telling the species apart (Carrel 2003a). In addition, burrow diameter, as measured with calipers to the nearest 0.1 mm, is a highly reliable surrogate for the size of the occupying spider as well as the depth and volume of its burrow (Tables 1 and 2).

Before a burn, I marked the location of each spider burrow (*n* = 700 total) by placing two thin metal stakes vertically in the sand ~10 cm on opposite sides of the burrow entrance. Following a burn, I revisited each burrow for 5 consecutive days and determined if the resident spider was alive. I used four criteria for survivorship: sighting of a spider sitting near the top of its burrow; luring a spider from the burrow by the presence of insect prey that I tethered on a thread near the entrance; restoration of a damaged burrow entrance or turret; and placement of newly excavated sand on the ground near a burrow. If all these criteria were negative, on the fifth or sixth day post-fire I carefully excavated a spider's burrow looking for its body. In so doing I could confirm that the burrow was occupied by a spider and, based on the soft, decomposing condition of a corpse, that the resident individual perished during or shortly after the blaze.

Air and soil temperature measurements.—I used Hobo U-12 digital dataloggers (Onset Computer Corporation, Pocasset, Massachusetts) fitted with Type K thermocouples to record air and soil temperatures in the scrub, following the established protocols of Wally et al. (2006). After calibrating each machine, I programmed the dataloggers in the laboratory to record one reading per second and to output maximum temperatures at 1 min intervals prior to deployment in the scrub. I obtained two sets of temperature data: maximum daily temperatures inside *G. x. archboldi* burrows and nearby

in undisturbed soil on hot, sunny days; and the intensity and duration of fire at point sites on the soil surface in oak scrub in order to gain a better perspective of the thermal dynamics experienced by subterranean spiders.

The first set of temperature recordings was designed to determine whether the open burrows of small and large *G. x. archboldi* under typical summer daytime conditions were significantly warmer than intact soil at comparable depths in the scrub. I chose to study only *G. x. archboldi* because this species occurs predominantly in large, barren gaps of unshaded sand where solar heating is the most intense in scrub. In contrast, *G. hubbelli* is typically found in small gaps with leaf litter on the sand, so its burrows are insulated from solar heating both by the leaf litter and by shade cast by the surrounding shrub matrix. Thus, my reasoning was that if maximum daytime temperatures in open *G. x. archboldi* burrows were comparable to those in undisturbed soil at comparable depths, then a similar burrow/soil equivalency probably would hold for *G. hubbelli* (even though the maxima obviously would be smaller). (Subsequent measurements showed this relationship was valid, JEC unpubl. data.) Over the course of 3 weeks in late August–early September 2007 I simultaneously set up ten replicate sets for 1 day each with thermocouples in five different positions: at 0, 5 cm, and 10 cm depth in intact sand and at the bottom of small (3–5 mm diam. \times 3.5–5.2 cm depth) and large (6–12 mm diam. \times 10.5–14.3 cm depth) *G. x. archboldi* burrows after the resident spiders were removed. Maximum daily air temperatures at 1.5 m above ground were also obtained at the official Archbold weather station on the days that soil temperatures were recorded.

Secondly, in an attempt to characterize the intensity and duration of a fire in oak scrub, I acquired data on soil surface temperatures during a “category 3” burn in August 2007 from the plant ecology group at Archbold. (“Category 3”, the highest intensity in the classification scheme used by Archbold staff, means that most surface litter was consumed, all leaves of palmettos and shrubs 0–2 m elevation were completely consumed, and small twigs on shrubs were consumed in a blaze.) Following their published protocol (Wally et al. 2006), many thermocouples attached to dataloggers were placed in contact with the soil surface at a variety of locations to record soil surface temperatures during a burn event. Using data from ten dataloggers in sites that experienced heavy burns, I normalized the temporal records so that the peak maximum temperatures all occurred at the 10 min mark, so that there would be several min of pre-burn data as well as ≥ 30 min post-maximum peak data. By definition, ignition threshold is $> 60^\circ\text{C}$ and cessation of fire is set at $\leq 60^\circ\text{C}$; the 60°C benchmark is used because it corresponds to the temperature at which plant cell death occurs (Wally et al. 2006, and references therein).

Statistical analyses.—I used the General Linear Models program of SPSS to perform ANOVA to evaluate the significance of variables in the sets of data on spider survival (SPSS 2005). The Levene test statistic was calculated to confirm that the variance did not differ significantly between the groups ($P > 0.05$). Differences in post-burn survivorship of spiders were analyzed by Chi square tests with Yates correction for small sample size (X^2_c , Simpson et al. 1960).

Table 3.—Effect of burn event, species identity and body size of spiders (as measured by burrow diameter) on post-burn survival of two *Geolycosa* species in Florida scrub.

Source of variation	df	MS	F	P
Burn event	6	0.178	1.966	0.068
Species	1	14.573	160.9	< 0.001
Size of spider	1	18.241	201.4	< 0.001
Species \times size	1	15.156	167.3	< 0.001
Error	672	0.091		

I calculated the average (mean \pm SE, $n = 10$) and range of maximum daily temperatures at all five locations in soil and in the air. I used the General Linear Models program of SPSS to perform univariate ANOVA to evaluate the significance of location in data on soil temperatures. The Levene test statistic was calculated to confirm that the variance did not differ significantly between the groups ($P > 0.05$). Subsequently I performed two post hoc multiple range tests (Student-Newman-Keuls (SNK) and Tukey HSD) to determine in a pairwise fashion which locations had significantly different temperatures (P set at 0.05) (SPSS 2005).

After normalizing the soil surface temperature data during one burn event so that temperatures peaked at all locations ($n = 10$) in the 10th minute, I calculated the minimum, mean, and maximum temperature minute by minute for 30 min.

RESULTS

Post-burn survival of *Geolycosa* species.—Spider species, spider size, and spider species \times spider size interaction were all highly significant variables determining the post-burn survival of *Geolycosa* species (Table 3). This meant that there was a complex interaction between spider species identity and spider size that required further analysis. Fortunately, as there were no significant differences among the seven burns according to the AVOVA results (Table 3), I was able to combine the data and delete “burn event” as a variable, which greatly simplified further analyses. As shown in Table 4, few small *G. hubbelli* (35.4%) survived the burns. In contrast, I found almost all large *G. hubbelli* (94.5%) and almost all *G. xera archboldi* regardless of size (small = 93.1%, large = 96.0%) were alive 5 days post-burn in the scrub. The intraspecific, size-dependent difference in survivorship for *G. hubbelli* was highly significant ($X^2_c = 133.49$, $df = 1$, $P < 0.0001$).

Maximum daily temperatures in *G. x. archboldi* burrows.—On ten sunny days in late summer 2007, maximum air temperatures at the Archbold weather station were hot, averaging $34.6 \pm 0.3^\circ\text{C}$ (mean \pm SE, range 33.3 – 36.1°C),

Table 4.—Survivorship of *Geolycosa* spiders as a function of burrow/body size and species identification. Results of statistical analyses (Chi square test with Yates correction for small sample size, X^2_c) for intraspecific size-based differences in survival are given.

Species	% Surviving		X^2_c	P
	Small ($n = 175$)	Large ($n = 175$)		
<i>G. xera archboldi</i>	93.1	96.0	0.89	NS
<i>G. hubbelli</i>	35.4	94.5	133.49	< 0.0001

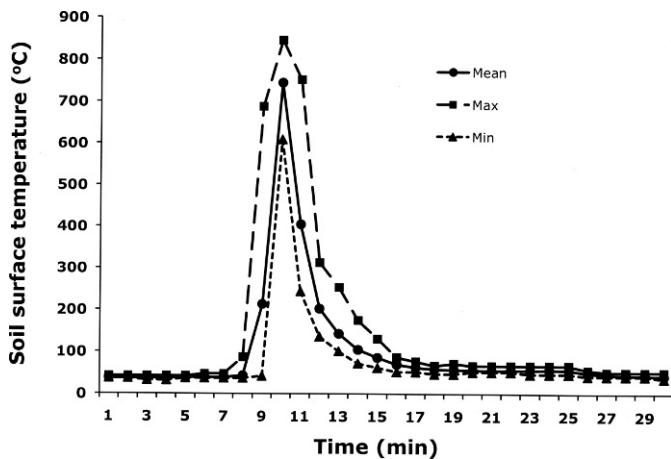


Figure 2.—Intensity and duration of a fire at a point source in Florida scrub. Note rapid onset and rise to peak temperature at soil surface, followed by somewhat less rapid decline. See methods for details.

but the maximum daily temperature on the surface of fully exposed sand in scrub was much greater: nearly 16°C hotter (51.2 ± 0.9 , $47.8\text{--}56.4^{\circ}\text{C}$). Univariate ANOVA showed there was a significant difference among the soil temperature data by location ($F_{4,45} = 3.599$, $P = 0.013$). Post hoc analysis revealed that, despite intense solar heating, the maximum daily temperatures at the bottoms of spider burrows and down in undisturbed soil remained significantly lower than at the surface (SNK and Tukey HSD tests, $P < 0.05$). Small, shallow spider burrows got as warm as soil at 5 cm depth (burrow: 38.5 ± 0.4 , $36.7\text{--}40.3^{\circ}\text{C}$; soil: 37.8 ± 0.5 , $35.7\text{--}40.0^{\circ}\text{C}$; $P = 0.44$). In addition, large, deep spider burrows stayed even cooler ($P < 0.05$) than shallow ones during the day and their maximum daily temperatures were the equivalent to those in soil at 10 cm depth (burrow: 33.3 ± 0.4 , $31.0\text{--}36.0^{\circ}\text{C}$; soil: 34.1 ± 0.4 , $32.7\text{--}36.0^{\circ}\text{C}$; $P = 0.28$). Hence, despite the fact that the spiders' burrows remained constantly open, the most extreme thermal climate experienced by resident animals if they were deep in the burrows would be virtually the same as if they were buried in undisturbed soil at a comparable depth, far less than that at the burrow entrance.

Soil surface temperature during a burn.—The time course of a burn in the scrub at any point in the burn unit was remarkably rapid. As shown in Fig. 2, the fire went from ignition temperature (60°C by definition) to peak maximum soil temperature ($609\text{--}846^{\circ}\text{C}$) in ≤ 2 min, then it declined to $\sim 60^{\circ}\text{C}$ in another 7 min. Hence, from the perspective of a *Geolycosa* hiding in its burrow, the fire lasted ≤ 10 min.

DISCUSSION

Mortality in *G. hubbelli*.—The results were generally in agreement with my initial hypotheses with one exception: the post-burn survivorship of large *G. hubbelli* was much greater than expected. In fact, to my surprise, it matched that for small or large *G. x. archboldi* (93–96%). I suspect burrow architecture makes large *G. hubbelli* very fire tolerant. As *G. hubbelli* grow they construct burrows that are not only wider in diameter and deeper, but also they excavate increasingly large, ovoid chambers at the bottoms (Table 1 and Fig. 1).

Such bulbous refugia ≥ 10 cm below the surface evidently protect large *G. hubbelli* from the brief but intense fires in the leaf litter and shrubbery above them, probably because the intense heat fails to penetrate to this depth.

I think the cause of mortality in small *G. hubbelli* is not fire-induced asphyxiation. Under natural conditions in sandy Florida soils, extensive measurements of prevailing gases in ~ 16 cm deep burrows occupied by a closely related burrowing wolf spider, *G. micranopy* Wallace 1942, showed no significant increases in CO_2 or decreases in O_2 concentrations relative to ambient atmospheric values (Anderson & Ultsch 1997). Thus, during a fire in Florida scrub, I doubt there would be extensive depletion of oxygen down in the spiders' porous burrows. Moreover, detailed physiological studies by Prestwich (1983a, b; 1988a, b) have demonstrated that active Florida spiders rely mostly on anaerobic metabolism because nearly all of their tissue phosphagen is quickly (within 10–15 s) depleted after onset of activity. Hence, a 10-min period of hypoxia during a fire in Florida scrub should, at best, present *Geolycosa* spiders at rest in their burrows only with a mild respiratory challenge.

I suspect the primary cause of fire-induced mortality in small *G. hubbelli* is high temperature in surficial soils and burrows. Field measurements show that soil temperatures at 2–3 cm depth rise to 80°C during intense fires in scrub, and at depths ~ 5 cm the temperature may reach 65°C when fuel-loads are modest (< 0.6 kg dry leaves and stems on the ground/ m^2) (Hierro & Menges 2002; Alexis et al. 2007). However, if the fuel-load on the ground in Florida scrub is high (~ 1 kg/ m^2), as often is the case near burrows of *G. hubbelli*, then maximum soil temperatures at 5 cm depth during a burn are very hot ($88 \pm 9^{\circ}\text{C}$) (Hierro & Menges 2002). Several other studies have reported similar relationships between fuel load and soil temperature profiles (Whelan 1995). Hence, the relatively shallow burrows of small *G. hubbelli* probably reach temperatures that exceed the upper lethal temperatures of spiders, which range from 45 to 55°C for most species (Pulz 1987; Hanna & Cobb 2007).

Assessment of fire effects on *Geolycosa* populations.—The strengths of this study are: 1. burn events were true replicates spanning 7 months of the calendar year; 2. pre- and post-burn sampling of many ($n = 700$) individual spiders was conducted; 3. sampling was size-based and quantitative. These attributes set it apart from almost all other previous studies that suffer from no replication or pseudoreplication and from nonquantitative or semiquantitative sampling methods (Warren et al. 1987; Siemann et al. 1997; Swengel 2001; van Mantgem et al. 2001; Hanula & Wade 2003). However, as explicitly pointed out by Whelan (1995), this study did not involve censuses of burrowing wolf spider populations before and after fires at randomly chosen sites. Thus, I cannot make any conclusions about whether fire has a significant impact on *Geolycosa* populations in Florida scrub. But the data in this study suggest fire probably is not at all deleterious to populations of *G. x. archboldi* and it may have only a weak negative effect in the short-term on *G. hubbelli* populations. Long-term studies still in progress will address this subject (JEC, unpubl. data).

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