Ecology of Two Burrowing Wolf Spiders (Araneae: Lycosidae) Syntopic in Florida Scrub: Burrow/Body Size Relationships and Habitat Preferences

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ABSTRACT: This fourteen year long study in the Florida scrub on the Lake Wales Ridge demonstrated that visually searching for open burrows of *Geolycosa* spiders was an effective method for sampling populations in the winter dry season, except one year when abnormally high precipitation during an El Niño event caused many spiders to close their burrows. Not only could the two endemic *Geolycosa* species be identified by the architecture of their burrow entrances (*G. xera archboldi* McCrone was aturricolous and *G. hubbelli* Wallace was turricolous), but the diameter of the burrow opening was highly correlated with the size of the resident spider and the volume of its burrow. The two syntopic *Geolycosa* species preferred different microhabitats: *G. xera archboldi* regardless of size was found in barren sand (0-10% litter coverage) whereas *G. hubbelli* shifted preference as it grew in size (going from 20 to 80% litter coverage). In addition each species exhibited significant habitat preferences: *G. xera archboldi* was most common in sand pine scrub with rosemary, the most xeric and least common habitat in the scrub; *G. hubbelli* was most abundant in scrubby flatwoods with sand live oak and in ridge sandhill with scrub hickory, both of which are relatively mesic sites with open canopies.

KEY WORDS: Spider, *Geolycosa*, syntopy, endemism, burrow, ecology, density, habitat, Florida scrub, El Niño

Introduction

The peninsula of Florida is exceptionally flat except for a series of ancient, sandy ridges extending along the coastlines and down the spine of the interior. Native scrub ecosystems found only on these xeric dunes are globally important centers of endemism, reflecting complex processes of evolutionary divergence dating back to the Pliocene and Pleistocene when fluctuations in sea level and other paleogeographic events alternately changed the area from a continuous, low lying land mass to an oceanic archipelago (Deyrup, 1989; Deyrup and Eisner, 1993, 1996; Eisner *et al.*, 1995; Menges, 1999). Most of the plants and animals endemic in scrub evidently are dependant on periodic fires to remove plant litter and to open up the tree and shrub layer, forming gaps for colonization. Because destruction of Florida scrub is proceeding rapidly, it is urgent that scientific studies be performed on the unique species in these communities so that land management questions can be answered (Kautz *et al.*, 1993; McCoy and Mushinsky, 1999; Menges, 1999).

Among the biota adapted to the seasonally dry conditions found in Florida scrub are burrowing wolf spiders in the genus *Geolycosa* (Araneae: Lycosidae). These spiders spend most of their lives in their burrows, whose circular entrances are very distinctive, and they possess limited dispersal abilities (Marshall *et al.*, 2000). The six *Geolycosa* species endemic to Florida scrub occur locally as species pairs; typically one species builds a turret of leaves anchored with silk around the burrow entrance and the other species does not build a turret (Marshall *et al.*, 2000). For example, in scrub on the southern part of Lake Wales Ridge in central Florida one finds both *G. xera archboldi* McCrone

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(aturricolous) and *G. hubbelli* Wallace (turricolous). Presumably the two species can exist syntopically because they use different microhabitats: *G. xera archboldi* is restricted to barren areas and *G. hubbelli* appears to occur only where there is a layer of leaf litter on the sand in gaps near vegetation (Marshall *et al.*, 2000).

The main purpose of this research was to determine the habitat preferences of syntopic *G. xera archboldi* McCrone and *G. hubbelli* Wallace in Florida scrub. Fortunately much is known about the ecology of *G. xera archboldi* because of the extensive studies of Sam Marshall that were performed at the same locality after my study was initiated (Marshall, 1995a, b, 1996, 1997, 1999; Marshall *et al.*, 2000), but to my knowledge little if any work has been performed with *G. hubbelli* since its original species description six decades ago (Wallace, 1942). In order to conduct robust field sampling of these *Geolycosa* species, I needed to verify that I could reliably locate and identify spiders while they were hidden in their burrows. Hence, over the course of fourteen years (1986-2000), I also performed a series of diagnostic measurements of spiders in relationship to various characteristics of their burrows.

Methods

Study Area

The Archbold Biological Station is located near the southern terminus of the Lake Wales Ridge in Highlands County, Florida (27°11′N lat., 81°21′W long.), 12 km south of the town of Lake Placid. The elevation ranges from approximately 36 to 67 m above mean sea level.

The Station is one of the largest (~2300 ha) and most representative tracts of scrub and sandhill habitats in peninsular Florida. Ten vegetative communities characterized by Abrahamson *et al.* (1984), as listed in Table 1 along with their code names, form a complex mosaic of habitats across the landscape. Scrubby flatwoods dominated by inopina oak, *Quercus inopina* Ashe (Fagaceae) (code name: SFi), is the most abundant habitat (~30% of total hectarage), whereas sand pine (*Pinus clausa* (Chapm. ex Engelm.) Vasey ex Sarq.) (Pinaceae) scrub with sandhill rosemary (*Ceratiola ericoides* Michx.) (Empetraceae) (SSr) is the rarest habitat (~2%).

In presettlement times, dating back at least 50,000 years, large landscape-scale fires occurred at fairly regular intervals on the Lake Wales Ridge (Myers, 1990). Most fires were started by lightning strikes associated with frequent thunderstorms early in summer following the long, winter dry season (Menges and Kohfeldt, 1995; Abrahamson and Abrahamson, 1996; Menges, 1999). The frequency of burns was habitat dependent: ridge sandhill with turkey oak (*Q. laevis* Walt.) (RSt), located at the highest elevations, tended to burn every few years, but the two kinds of sand pine scrub (SSr and SSo) might not burn for nearly a century (see Table 1). The spatially heterogeneous burn pattern largely disappeared after 1880 when settlers thoroughly suppressed fires. To restore the natural burning cycles appropriate for the various habitats, staff scientists at the Station developed and instituted a comprehensive fire management program in the 1980's (Main and Menges, 1997). The overarching assumption is that all species listed as threatened or endangered will benefit from natural burn processes.

The Spiders and Their Burrows

The genus *Geolycosa* is found throughout North America, but its center of diversity is Florida: nine of 18 recognized nearctic species or subspecies are found in this state (Wallace, 1942; McCrone, 1963; Gertsch, 1979; Marshall *et al.*, 2000). The burrows and burrow-associated behavior of *Geolycosa* are unique among wolf spiders, which makes their identification almost unmistakable (Wallace, 1942). *Geolycosa* burrows consist of nearly vertical, cylindrical tubes, 2–30 mm diameter, that extend to a depth of 3–60 cm (Hancock, 1899; Wallace, 1942; Edwards and Edwards, 1989; Corey, 1991).

Table 1. Relative abundance and natural burn frequency of ten major habitats based on vegetation types at the Archbold Biological Station. *

Code name	Full name (Association-phrase)	% Total area	Modal fire-return interval (years)
TP	Temporary ponds	10.7	6-9
FLp	Flatwoods-palmetto	9.8	6-9
FLg	Flatwoods-gallberry	5.3	6-9
FLw	Flatwoods-wire grass	9.2	6-9
SFl	Scrubby flatwoods-sand live oak	6.5	10-19
SFi	Scrubby flatwoods-inopina oak	30.1	6-9
SSo	Sand pine scrub-oak understory	9.0	20-59+
SSr	Sand pine scrub-rosemary	2.3	20-59
RSh	Ridge sandhill-scrub hickory	8.6	10-19
RSt	Ridge sandhill-turkey oak	5.6	2-5
	Subtotal	97.1	

*Based on data in Abrahamson et al. (1984) and Main and Menges (1997).

The entrances of *Geolycosa* burrows are very circular, more so than those of almost all other terrestrial arthropods (J. Carrel, pers. obs.), and, depending on the species, the openings may or may not be adorned with turrets made of debris fastened with silk. Only adult male spiders leave their burrows and wander in search of mates; immature and female *Geolycosa* remain in their burrows most of the day and night, emerging briefly to capture prey or to deposit excavated soil (Emerton, 1912; Wallace, 1942; McCrone, 1963). As spiders grow they enlarge their relatively permanent burrows (Emerton, 1912). Hence, as documented by several investigators, burrow diameter is highly correlated with body mass or carapace width in *G. domifex* (Hancock), *G. escambiensis* Wallace, *G. micanopy* Wallace, *G. ornatipes* (Bryant), *G. patellonigra* Wallace, G. *turnicola* (Treat), *G. xera xera* McCrone, and *G. xera archboldi* McCrone (McQueen, 1978; Miller and Miller, 1984; Corey, 1991; Marshall, 1999).

G. xera archbold and *G. hubbelli* are moderately large wolf spiders: body length in adult females is 12–15 mm. *G. xera archboldi* is covered with a whitish-gray bubescence, so it s cryptic on the white sands in Florida scrub. In contrast, *G. hubbelli* is dark brown or black except for a yellow or gray median stripe on the carapace and dorsum of the abdomen, so it blends in well when resting on a background of leaf litter. Both species have very restricted distributions in central Florida: *G. xera archboldi* is found only in Highlands Co., and *G. hubbelli* occurs as three disjunct populations in Highlands, Orange, and Marion Co. (Wallace, 1942; McCrone, 1963; Marshall *et al.*, 2000).

Species Specificity and Apparency of Spider Burrow Entrances

The literature states that *G. hubbelli* always builds a turret from leaf litter at the entrance to its burrow but *G. xera archboldi* does not build a turret of any kind (Wallace, 1942; Marshall *et al.*, 2000). to determine the reliability of the turricolous/aturricolous trait as a species-specific indicator, from 1987 to 1998 I located a total of 100 putative *G. hubbelli* burrows having turrets and 100 putative *G. xera archboldi* burrows without turrets in most of the different habitat types. I carefully excavated each burrow to extract the resident spider and identify it. I used a chi-square analysis to test statistically the relationship between turret presence/absence and spider species identity.

Because *Geolycosa* burrows are small (2–18 mm diameter) and often constructed near or underneath various shrubs where there may be a layer of leaf litter, I performed the following test to assess the apparency of spider burrows to a human observer walking through the scrub. In 1989 I established ten quadrats (2x2 m) in the scrub where each species was locally abundant. I then visually searched each of the 20 quadrats for 2-3 min while I crept slowly forward, bent over so my head was ~1 m above the soil. I gently moved any over hanging vegetation so that I could inspect the ground beneath it. The location of a spider burrow was marked with a flag. Subsequently, on the same day, I revisited the same quadrat and inspected it again at a height of only ~0.3 m while on my hands and knees, removing all of the leaf litter carefully with forceps, in order to locate any spider burrows that I might have missed. The close inspection took 5–10 min at a barren site with *G. xera archboldi* and 20–30 min at a litter-covered site with *G. hubbelli*.

Leaf Litter Coverage around Spider Burrows

Supposedly the two syntopic species of *Geolycosa* prefer distinctly different scrub/sandhill microhabitats: *G. xera archboldi* burrows only in open sand whereas *G. hubbelli* selects sites that have a well developed layer of leaf litter (Marshall 1995a, 1997; Marshall *et al.*, 2000). To evaluate this generalization, I determined if the amount of leaf litter on the ground around the entrance of a *Geolycosa* burrow was species- and size-dependent. In Feb. 1992 I walked 5.3 km from the north boundary of the Station in tract 6 southward through tracts 7, 18, and 19. Scrubby flatwoods and flatwoods comprised 75% of the habitats encountered along this transect. Whenever I encountered an open *Geolycosa* burrow, I identified the species, measured the diameter of its entrance (to the nearest 0.1 mm) with calipers and then estimated the percent leaf litter coverage to the nearest 10% within a 10 x 10 cm frame centered on the burrow.

I sorted the data for spider burrows into mm-size classes. For example, burrows whose diameter ranged from 3.6 to 4.5 mm were lumped into the 4 mm size class. Within each size class I calculated the median percent litter coverage because the data were not normally distributed (Zar, 1974). I used linear regression analysis to test if median percent litter coverage varied as a function of burrow diameter for each species.

Diameter of Spider Burrows as a Size Indicator

I hypothesized that the diameter of the entrance to a burrowing wolf spider's burrow might be a robust, handy indicator of the spider's body size and, perhaps, even of the volume and depth of its burrow. If this proved to be true, then one could learn much about the age-structure of a population simply by this simple, nondestructive measurement without actually examining spiders. I performed two tests to evaluate these ideas.

First, over the course of several years (Feb. 1987, 1993, and 1998) I excavated 50 individuals each of *G. xera archboldi* and *G. hubbelli* in the scrub after I measured the diameter of a burrow entrance (to nearest 0.1 mm) with calipers. I put spiders individually in cool vials and took them to the lab whereupon I immediately weighed them on an analytical balance (to the nearest 0.1 mg) and then measured the width of the carapace (to nearest 0.1 mm) using an ocular micrometer. I also examined spiders to determine whether they were immatures, juvenile females, or females. I never encountered any adult or subadult male spiders of either species.

Second, in Feb. 1986, 1994, and 1996 I determined the depth and volume of 25 *G. xera archboldi* and 30 *G. hubbelli* burrows after I had measured the diameter of the burrow entrances with calipers. I lured a spider from its burrow by placing a mealworm tied to thread at the opening. Spiders often

rushed out to bite the prey, but others waited to attack until the insect had crawled into the burrow. Regardless of the mode of attack, after I removed a spider while it bit the tethered larva, I then gently injected watery plaster of Paris into the burrow and let it dry in situ for 2-3 days before I carefully excavated the cast and brought it to the lab. After the plaster had dried at room temperature for several weeks, I measured the length of each cast (to the nearest mm) with a ruler to determine burrow depth in the soil and then I used the classical water displacement method to determine the volume (to the nearest ml) of each cast.

In both studies I used linear regression analyses of untransformed and log-transformed data to quantify relationships between variables. For example, if one assumes a spider's burrow is a modified cylinder, then the geometric equation indicates that the log of the volume should increase as a function of the log of the burrow diameter.

Abandonment of Burrows by Spiders

Results of studies with *G. xera archboldi* performed in spring and summer at the Station indicated that members of this species, especially spiderlings, frequently (~2%/day) abandon their burrows and build new ones (Marshall, 1995a). If this were to hold for both *Geolycosa* species in winter, when I did my field work each year, then the frequency of open spider burrows might be much higher than the actual spider population. The presence of many unoccupied, open burrows would make it difficult or impossible to census spider populations using burrow counts. I hypothesized that the turnover rate of spider burrows in the cool, dry season might be relatively low and that it might be confined primarily to small spiders as they disperse from the natal burrow and set up their own burrows. I reasoned that naive spiderlings not only might build burrows in microhabitats that soon prove inappropriate, but they also could inadvertently invade territories of older, more "established" conspecifics at good sites. For these reasons, I anticipated that burrow relocation would be size dependent.

To assess rates of burrow abandonment by spiders, in Feb. 1996 I located 100 open burrows each of *G. xera archboldi* and *G. hubbelli*, 20 of each species at five different sites in scrub separated from one another by at least 0.5 km. The location of each burrow was marked with a surveyor flag and the diameter of its entrance was measured with calipers. I determined that the burrow was occupied either (1) by observing a spider in its burrow, (2) by detecting freshly excavated, moist sand on the ground near the burrow entrance, or (3) by baiting a spider from its burrow with a tethered mealworm. To estimate spider population density according to Pielou's formula (cited in Marshall, 1995a), I measured the distance to the nearest neighboring *Geolycosa* burrow. After 14 days I again located each burrow. I noted whether the burrow was open or closed. Subsequently I determined whether the burrow was still occupied. If the three criteria used previously were negative, then I carefully excavated the burrow to verify the presence or absence of a resident spider.

Closure of Burrows by Spiders

Although *Geolycosa* are typified as having open burrows, my preliminary observations made during cold spells and heavy rainstorms revealed that these spiders can rapidly close their burrow entrances until weather conditions improve. In addition, Marshall (1995a) found *G. xera archboldi* during spring and summer often close their burrows for about 7 days in a row. To determine the rate of burrow closure by *Geolycosa* in winter at the Station, for nine years (February, 1992–2000) I annually located 200 open burrows of each species in different regions of the scrub and then returned in 7 days to ascertain whether a burrow was open or closed. Using these data, I calculated the average frequency of burrow closure for each species.

Table 2. Presence or absence of a turret at mouth of burrow is a reliable species-specific indicator for burrowing wolf spiders.

Turret at burrow	Resident species *			
	G. xera	*G. hubbelli*	No spider	Total
Absent	96	2	2	100
Present	0	99	1	100

* $\overline{X}^2$ = 189.49, d.f. = 2, *P* < 0.0001.

Habitat Distribution of Spiders

I systematically determined the density of burrowing wolf spiders in ten habitats (Table 1) during one week in Feb. 1993 using a randomly stratified sampling scheme. I overlaid a vegetation map of the Station (Abrahamson *et al.*, 1984; E. Menges, unpubl.) with a transparent grid sheet and then used a table of random digits to identify intersection points within nine tracts (SW, SE, 6, 7, 18, 18E, 19, 30, and 31) that had been burned 1–13 years beforehand. I selected ten replicate sites in the ten habitat types, for a total of 100 sites. I went to each site during daytime, walked a randomly predetermined number of paces (5–20) into it according to the polygons on the vegetation map, turned in a randomly predetermined compass direction (N, S, E, W), and extended a 10 m tape in that direction. I spent ~0.5 hr censusing the number of *Geolycosa* burrows located 1 m on either side of the tape, forming a 2 x 10 m (=20m^2) quadrat.

I performed a fully factorial (M)ANOVA in SYSTAT (Wilkinson, 1989) to test whether the density of each spider species was significantly different among the ten habitats. Subsequently I used a post-hoc contrast to test the influence of single habitat types on the outcome of the ANOVA.

To evaluate habitat preferences in the two *Geolycosa* species, I employed a chi-square goodness-of-fit test in conjunction with Bonferroni confidence intervals (Neu *et al.*, 1974; Byers *et al.*, 1984) to analyze my utilization-availability data. This approach can detect whether a particular habitat is being preferred or avoided by the spiders.

Results

Species Specificity and Apparency of Spider Burrow Entrances

The presence or absence of a turret at the entrance to a spider's burrow proved to be a very reliable indicator of species identity for the two *Geolycosa* species found at the Station. As indicated in Table 2, 96% of burrows lacking turrets were occupied by *G. xera archboldi* and 99% of burrows having turrets were occupied by *G. hubbelli*. Examination of the excavated spiders revealed that most individuals were immatures and some were adult females, but none were adult males.

The fact that only three of 200 burrows were empty suggested that burrow abandonment by either *Geolycosa* species might happen infrequently in winter, unlike the findings of Marshall (1995a). A direct test of this idea is reported in a subsequent section.

Laborious follow-up observations made at ground level showed that almost all *Geolycosa* burrows were apparent to a trained observer creeping through the scrub even when leaf litter was present on the ground. Initial inspection of ten 4 m^2 quadrats for each species yielded a total of 43 *G. xera*

Table 3. Comparison of size of female *Geolycosa* and their burrow entrances. Values represent means ± SEM and the outcome of pairwise Student's *t*-tests.

Species	*N*	Body mass (mg)	Carapace width (mm)	Burrow diameter (mm)
G. xera archboldi	15	154 ± 14	3.55 ± 0.10	7.95 ± 0.23
G. hubbelli	16	292 ± 35	4.47 ± 0.17	12.60 ± 0.35
t		3.59	4.55	10.98
P	0	<0.01	<0.001	<0.0001

archboldi and 56 *G. hubbelli* burrows. A second, detailed inspection near the ground, one that included manual removal of all litter, yielded only one additional *G. xera archboldi* burrow and three additional *G. hubbelli* burrows (one each in three quadrats). Thus, during the initial, fairly rapid inspection 97.7% of *G. xera archboldi* and 94.9% of *G. hubbelli* having open burrows were detected.

Leaf Litter Coverage around Spider Burrows

There was a pronounced difference between the two *Geolycosa* species with regard to the amount of leaf litter in the vicinity of their burrows. A total of 220 *G. xera archboldi* and 315 *G. hubbelli* burrows were examined on a long transect through the scrub. As indicated in Fig. 1, little leaf litter (0–10% coverage) was found around burrow entrances of *G. xera archboldi* regardless of size. In contrast, the extent of leaf litter around the burrows of *G. hubbelli* was related positively to the diameter of the burrow entrance ($R=0.87$, d.f. = 13, $P < 0.001$), and hence, the size of the resident spider. Small *G. hubbelli* burrows (2–3 mm diameter) had little leaf litter near them (~20% coverage), but large *G. hubbelli* burrows (11–15 mm diameter) had much litter (~80% coverage) within 5 cm from the entrance. Thus, small individuals of *G. hubbelli* evidently colonized gaps having relatively open sand that were not much different from those favored by *G. xera*, but larger individuals were found in areas with a thin, more-or-less complete layer of leaves mixed with other dead plant tissues.

Diameter of Spider Burrows as a Size Indicator

Spider body mass (log-transformed) was highly correlated with carapace width in both *Geolycosa* species excavated from the soil (*G. xera*: $R = 0.98$, d.f. = 49, $P < 0.001$; *G. hubbelli*: $R = 0.94$, d.f. = 49, $P < 0.001$). Furthermore, as shown in Fig. 2, these two parameters were also strongly correlated with the diameter of a spider's burrow. Therefore, burrow diameter was a good predictor of the size of a spider hidden deep in its burrow. In addition, all individuals of *G. xera archboldi* having burrows ≥7 mm diameter, upon microscopic examination, were found to be adult females; the same was true for *G. hubbelli* whose burrows were ≥11 mm diameter. Analysis of the data for adult spiders revealed that female *G. hubbelli* were significantly larger and built bigger burrows than female *G. xera archboldi* (Table 3).

In both *Geolycosa* species there was a positive exponential relationship between the diameter of a spider's burrow entrance and the volume of its burrow based on the measurements using plaster casts of evacuated burrows (*G. xera archboldi*: y = –2.1754 + 3.6362 x; *G. hubbelli*: y = –1.3670 + 2.5992 x, where y is log ml and x is log mm). The correlation coefficient for the *G. xera archboldi* data was remarkably large ($R = 0.974$, d.f. =24, $P < 0.0001$) because most burrows were highly cylindrical. On the other hand, there was greater scatter in the *G. hubbelli* data ($R = 0.894$, d.f. = 29, $P < 0.0001$) because large burrows tended to have bulbous bottoms whose shapes and sizes varied a lot.

Table 4. Density and rate of burrow abandonment by burrowing wolf spiders (*N* = 20 of each species at five sites) in winter.

Site	G. xera		G. hubbelli	
	Mean density (#/m²)	Rate of abandonment (%/day)	Mean density (#/m²)	Rate of abandonment (%/day)
A	0.30	1.07	0.20	0.36
B	0.19	0.71	0.50	0
C	0.19	1.07	0.05	0.71
D	0.16	0	0.08	0.36
E	0.08	0.36	0.05	0
X̄ ± SEM	0.18 ± 0.03	0.64 ± 21	0.18 ± 0,08	0.29 ± 0.13

The difference in burrow architecture between the two spider species was evident when variation in burrow depth was considered. Burrow depth in *G. xera archboldi* increased as a linear function of burrow diameter (y = –0.8572 + 1.8072 x, where x is mm and y is cm; *R* = 0.925, d.f. = 24, *P* < 0.0001). In contrast, burrow depth in *G. hubbelli* was positively related to the log of burrow diameter (y = –1.8937 + 15.725 (log x); *R* = 0.649, d. f. = 29, *P* < 0.001), reflecting the fact that as spiders of this species reached maturity their burrows were not deepened even though burrow volumes were increased. Species differences in burrow size and shape were most evident when only casts of adult females were considered. There were casts of burrows made by 14 *G. xera archboldi* and 15 *G. hubbelli* included in my nonrandom samples. The average diameter of female *G. xera archboldi* burrows (9.0 ± 0.4 mm) was significantly less than the average diameter for female *G. hubbelli* (13.3 ± 0.6 mm) (*t* = 5.84, d.f. = 27, *P* < 0.001). Likewise, the average volume of burrows constructed by female *G. xera archboldi* (21.4 ± 3.5 ml) was significantly less that the average volume for female *G. hubbelli* (33.1 ± 3.1 ml) (*t* = 2.50, d.f. = 27, *P* < 0.02). However, there was no significant difference between the mean depths of burrows for female *G. xera archboldi* (15.4 ± 3.5 cm) and female *G. hubbelli* (14.9 ± 0.6 mm) (*t* = 0.46, d.f.= 27, *P* > 0.6).
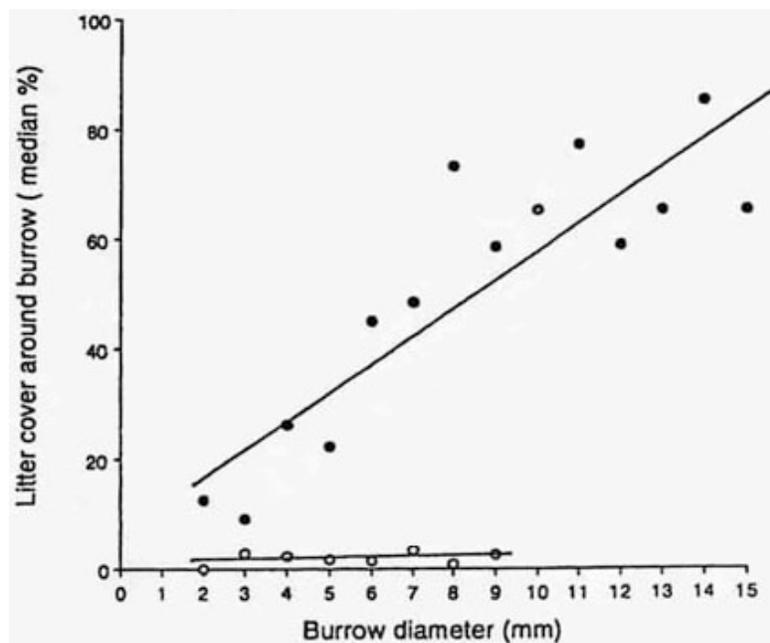

Fig. 1. Amount of leaf litter in a 10 x 10 cm area centered on burrows of *Geolycosa hubbelli* (solid circles) in Florida scrub increased as a function of the width of the spiders' burrow entrance (y = 7.523 + 5.087x, R = 0.873, d.f. = 13, P < 0.001). In contrast, the amount of leaf litter near burrows of *G. xera archboldi* (open circles) reminded near zero regardless of burrow size (y = 1.212 + 0.1224x, R = 0.261, d.f. = 7, P > 0.1).

Table 5. Nearest neighbor relationships of burrowing wolf spiders in scrubby flatwoods.

	Nearest neighboring species *		
Resident species	G. xera	G. hubbelli	Total spiders
G. xera	84	16	100
G. hubbelli	14	86	100

* X^2 = 98.33, d.f. = 1, P < 0.0001.

Abandonment of Burrows by Spiders

The results of replicated field tests (Table 4) reveal that both *Geolycosa* species abandoned their burrows at a low rate (<1%/day) in winter, well below the value (~2%/day) for *G. xera archboldi* reported by Marshall (1995a). Although on average *G. xera archboldi* vacated burrows twice as frequently as *G. hubbelli* (0.64 versus 0.29% burrows/day, respectively), this difference was not significant (Mann-Whitney test, *U* = 18.5, *P* > 0.2). Mean density of both *Geolycosa* species at the test sites in scrub was identical, 0.18 spiders/m², ranging from 0.05 to 0.50 spiders/m². Moreover, rate of burrow abandonment by each species was not correlated with spider density at a site (*R* ≤ 0.66, d.f. = 4, *P* > 0.1). At all five sites the nearest neighbor of any individual *Geolycosa* usually was a conspecific spider (Table 5), a reflection of the spiders' tendency to aggregate in different microhabitats which results in local segregation of the two species. Hence, if I found a burrow of one species, I was very likely (~85% of cases) to find another burrow of the same species nearby.
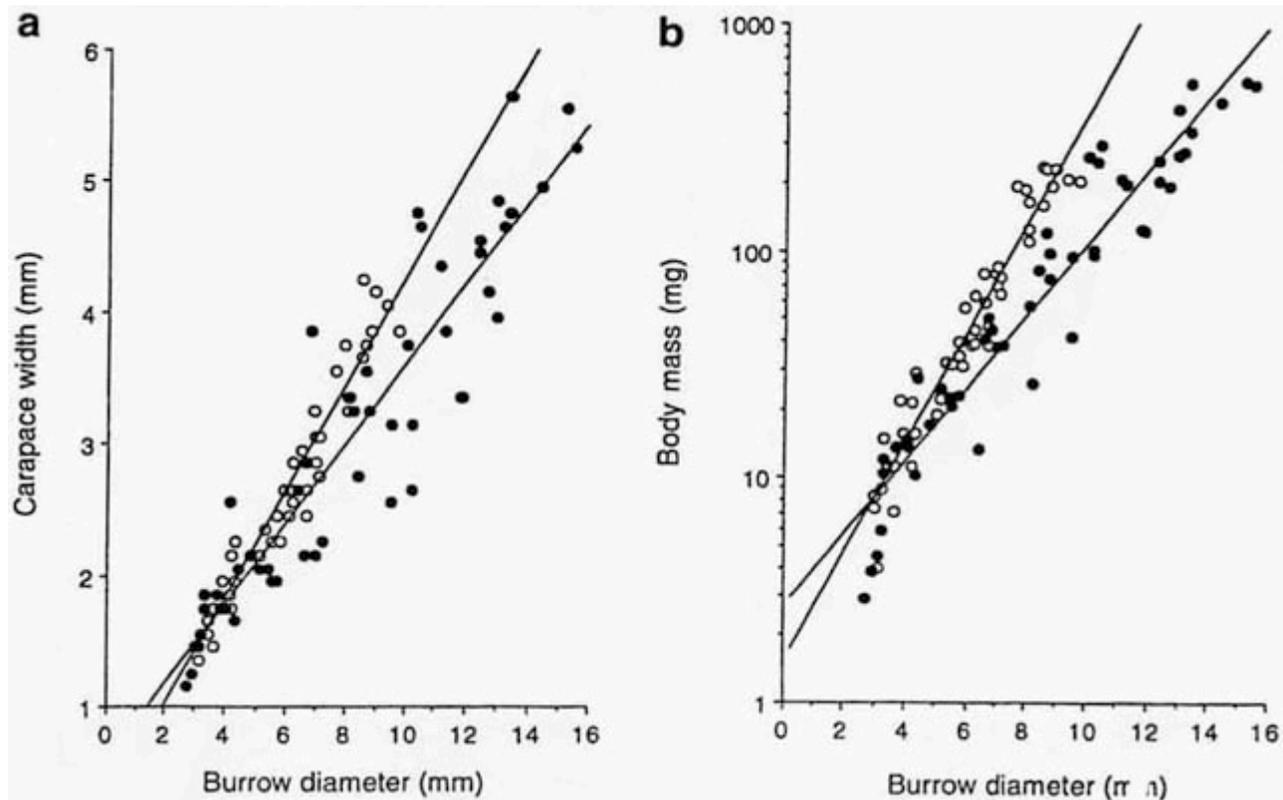

Fig. 2. Size of *Geolycosa xera archboldi* (open circles) and *G. hubbelli* (solid circles) was positively related to the width of their burrow entrances. (a) Carapace width in *G. xera archboldi* (y = 0.229 + 0.405x, *R* = 0.968, *P* < 0.001) and in *G. hubbelli* (y= 0.571 + 0.305x, *R* = 0.922, *P* < 0.001). (b) Wet body mass in *G. xera archboldi* (y = 1.602 * $10^{0.24114x}$, *R* = 0.966, *P* < 0.001) and in *G. hubbelli* (y = 2.727 * $10^{0.15931x}$, *R* = 0.954, *P* < 0.001).

Table 6. Relative frequency (%) of burrow closure in burrowing wolf spiders during nine winters (N = 200 burrows/species/year).

Year	G xera	G. hubbelli
1992	5.5	3.5
1993	3.5	0.5
1994	9.5	1.0
1995	3.0	1.5
1996	8.0	2.5
1997	3.5	2.5
1998	22.0	5.5
1999	6.5	3.0
2000	6.0	2.0
$\overline{X}$ ± SEM	7.5 ± 2.0	2.4 ± 0.5

Abandonment of burrows was most prevalent in small *Geolycosa*. Eight of nine *G. xera archboldi* burrows that were vacant after 2 weeks were 3–5 mm in diameter. Likewise, three of four vacant *G. hubbelli* burrows were in the 3–4 mm size class. Hence, small spiders vacated burrows at a much higher rate than large spiders (0.86%/day versus 0.14%/day, respectively.

Closure of Burrows by Spiders

Based on nine years of observation, only a small percentage of *Geolycosa* kept their burrows closed in winter (Table 6). Every year *G. xera archboldi* had a significantly higher proportion of closed burrows than *G. hubbelli* (7.5% versus 2.4%, respectively, Mann-Whitney test, U = 75, P < 0.002). The data for 1998 represent an interesting anomaly. Burrow closure rates for spiders in 1998 were twice as high as in any other year because a strong El Niño event resulted in record winter rainfall (18.24 cm in Jan.–Mar. 1998), which was 3.5 times greater than the 30-year winter average (5.22 cm) for the Station.

Habitat Distribution of Spiders

The density of *Geolycosa* at the 100 randomly chosen sites ranged from 0 to 1.7 spiders/m². Analysis of variance (Table 7) revealed that habitat, species, and the habitat × species interaction all were significant variables (F > 5.39, P < 0.005). Thus, the two species of spiders exhibited different habitat distributions. A post-hoc contrast using ANOVA showed that *G. xera archboldi* was very abundant (0.49 ± 0.16 spiders/m²) in the sand scrub with rosemary (SSr) habitat, but relatively uncommon or absent from all other habitats. The overall pattern is depicted in Fig. 3. In contrast, even though *G. hubbelli* was most prevalent (0.36 ± 0.07 spiders/m²) in ridge sandhill with scrub hickory (RSh), it also was fairly common (>0.05 spiders/m²) in eight of nine remaining habitat types. These results suggest *G. xera archboldi* is an extreme habitat specialist whereas *G. hubbelli* is more of a habitat generalist.

According to a chi-square test on the utilization-availability data, there was a highly significant difference between the expected and observed frequency of *Geolycosa* in the different scrub and sandhill habitats ($\overline{X}^2$ = 1315.0, d.f. = 9, P << 0.0001). Using the Bonferroni confidence intervals (Table 8), three patterns in habitat usage were evident. First, spiders preferred three habitats: *G. xera archboldi* was more abundant in sand pine scrub with rosemary (SSr) and *G. hubbelli* was more abundant in scrubby flatwoods with sand live oak (*Q. geminata* Small) (SFl) and in ridge sandhill with scrub hickory (*Carya floridana* Sarg.) (RSh) than expected. Second, the spiders avoided three habitats:

Table 7. ANOVA table for the abundance of two burrowing wolf spiders in ten different scrub and sandhill habitats (N = 10 replicate quadrats per habitat). R^2 = 0.413.

Source	d.f.	Mean-square	F-ratio	P
Habitat	9	50.622	5.391	<0.0001
Species	1	74.420	7.925	0.005
Habitat x species	9	73.309	7.807	<0.0001
Error	180	9.390		

both *Geolycosa* species were less common in dehydrated temporary ponds (TP), scrubby flatwoods with inopina oak (SFi), and in ridge sandhill with turkey oak (RSt) than expected. Finally, the spiders were found in four habitats as frequently as expected based on random usage patterns: all three kinds of flatwoods (FLp, FLg, FLw) and sand pine scrub with various shrubby oaks (SSo).

Discussion

Validation of Sampling Method

Background studies, which were performed annually in February for 14 years, showed that visually searching for open burrows usually was an effective method for estimating densities of two *Geolycosa* species in Florida scrub. If one adjusted for burrow closure (Table 6), apparency of open burrows, and the reliability of a turricolous/aturricolous burrow entrance as an indicator of occupancy by a given species (Table 2), then it was estimated that 87% of *G. xera archboldi* and 92% of *G. hubbelli* individuals living in an area were detected in a single search. Moreover, because *Geolycosa* typically keep their burrows closed for fewer than 7 days at a time (Marshall, 1995a; J. Carrel, unpubl. obs.), a second search of an area performed a week of so after the first inspection would permit detection of 95% of *G. xera archboldi* and 94% of *G. hubbelli* individuals, which in effect would be an actual census of a local population of burrowing wolf spiders. Only during the strong El Niño event in the winter of 1998 did many spiders close their burrows, much as they routinely do during the rainy season from April to September (Marshall, 1995a).

Sampling spider populations in nature is difficult. Commonly used methods, such as sweep netting, vegetation beating and pitfall trapping, are at best semiquantitative and, at the community level, they are not generally robust measures of spider presence and abundance in a habitat (Churchill and Arthur, 1999; Norris, 1999; Sørensen *et al.*, 2002, and references therein). Recently it was shown that searching for dew-laden cobwebs at dawn on foggy mornings enabled detection of 90% of red widow spiders, *Latrodectus bishopi* Kaston, in Florida scrub (Carrel, 2001). This result is comparable to the rate of finding *Geolycosa* as reported here. Hence, it may be possible to census rigorously populations and guilds of spiders that construct distinctive, easily seen webs or burrow entrances.

Size of Spiders and Their Burrows

Burrows constructed by *G. hubbelli* were larger in diameter than those made by *G. xera archboldi* in large part because *G. hubbelli* is inherently bigger than *G. xera archboldi* (Table 3). In addition, species-specific differences in morphological variation may result in *G. hubbelli* having larger burrows. As shown in Fig. 2a, the rate of increase in burrow diameter as spiders grew in carapace width was greater for *G. hubbelli* than for *G. xera archboldi*. This probably arose because allometric growth in the two species is different: *G. hubbelli* appears to have relatively longer legs and a heavier body than does

Table 8. Utilization-availability data and simultaneous confidence intervals using the Bonferroni approach for utilization of habitats by burrowing wolf spiders.

Habitat code name	Expected proportion of usage, P_{io}	Actual proportion of usage, P_i	Bonferroni intervals for P_i*				
TP	0.110	0.061	0.026	≤	P_{TP}	≤	0.095 *
FLp	0.101	0.071	0.034	≤	P_{FLp}	≤	0.108
FLg	0.055	0.037	0.010	≤	P_{FLg}	≤	0.064
FLw	0.095	0.063	0.028	≤	P_{FLw}	≤	0.098
SFl	0.067	0.116	0.070	≤	P_{SFl}	≤	0.162 *
SFi	0.310	0.090	0.048	≤	P_{SFi}	≤	0.131 *
SSo	0.093	0.076	0.038	≤	P_{SSo}	≤	0.115
SSr	0.024	0.295	0.229	≤	P_{SSr}	≤	0.360 *
RSh	0.089	0.187	0.131	≤	P_{RSh}	≤	0.243 *
RSt	0.058	0.005	0	≤	P_{RSh}	≤	0.016 *

* Indicates a difference at the 0.05 level of significance.

G. xera archboldi. Shape variation and its relationship to evolutionary ecology has been studied recently in many vertebrates due to a revolution in geometric methodology (Losos, 1990; Rohlf and Marcus, 1993; Ricklefs and Miles, 1994; Adams, 1999; Rüber and Adams, 2001), but this type of analysis seems not to have been applied to spiders. Ecomorphometric studies are underway currently to determine the relationships between body shape and burrow construction in *Geolycosa* (J. Carrel, in progress).

Both species of *Geolycosa* built narrow (2–4 mm diameter), shallow (3–6 cm depth), low volume (0.3–2 ml) tubular burrows in the sandy scrub soils when they were small. As they grew in size and approached adulthood, spiders of both species deepened and widened their burrows until they were about 12 cm in depth, at which time the diameter of the entrance was 6–8 mm and the volume was ~8ml. Thereafter, the two species of spiders followed somewhat different trajectories in burrow construction. *G. xera archboldi* females in direct proportion to their body size, like immature conspecifics, excavated deeper burrows while they created a bulbous cavity at the bottom. On the other hand, regardless of their size, *G. hubbelli* females did not deepen their burrows very much; instead they greatly enlarged the burrows, particularly the middle and bottom portions. Thus, the range in burrow depth was greater for *G. xera archboldi* females (9.2–23.4 cm) than for *G. hubbelli* females (11.5–20.1 cm) although the latter species on average had much more voluminous burrows (Table 3). A similar contrast in burrow architecture between two species of burrowing wolf spiders (*G. turricola* and *G. pikei*) appears to exist where they are syntopic on Cape Cod, MA (Edwards and Edwards, 1989).

There are obvious benefits and costs of having a deep, large burrow for a burrowing wolf spider. For example, daily fluctuations in soil temperature are much less at 15 cm depth than at 2.5–5 cm depth in sandy scrub soils (Carrel, 1980), so having a deep retreat would allow a spider to live in a thermally buffered zone and still have good exchange of respiratory gasses (Anderson and Ultsch, 1987). In addition, deep burrows should allow protection from enemies, such as armadillos and ants, and from drowning during heavy rainstorms. On the other hand, if a spider rests 12–20 cm below ground, it may not detect passing prey that it otherwise would sense while sitting near the soil surface. Deep burrows require much time and energy to excavate and to maintain, especially when the wind blows sand into the burrow entrance or when a lower part of the burrow collapses as the sand dries (Halloran *et al.*, 2000). Perhaps *G. xera archboldi*, lacking a turret, frequently closes its burrows mainly to prevent the entrance of sand grains blown by breezes that routinely sweep across barren gaps in the scrub, much as is done by a northern species (*G. wrightii* (Emerton)) that inhabits dunes by the Great Lakes (Gwynne and Watkiss, 1975).
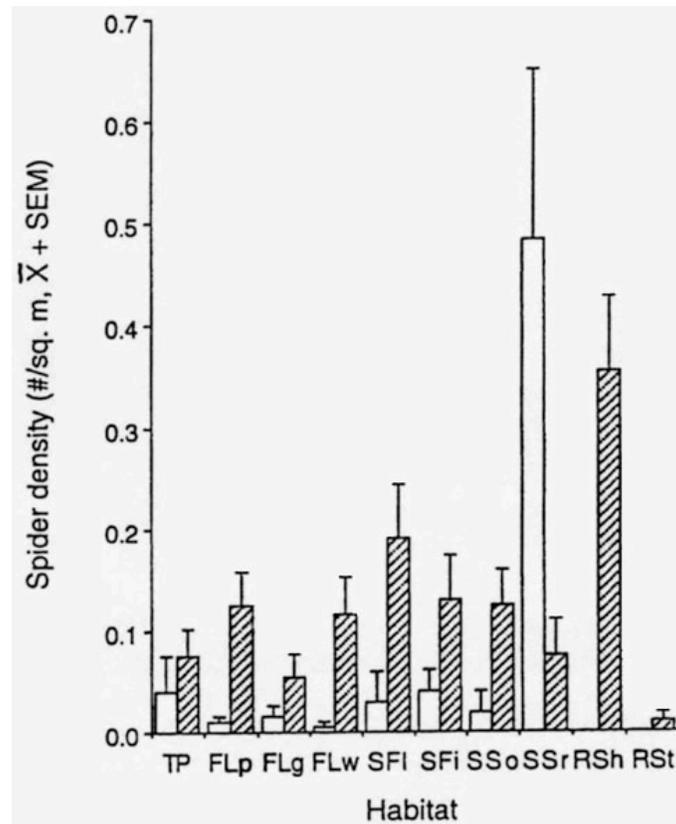
Fig. 3. Average density (# burrow/m²) of *Geolycosa xera archboldi* (open bars) and *G. hubbelli* (shaded bars) in ten habitats in the Florida scrub at the southern terminus of the Lake Wales Ridge, Highlands Co. Data represent means + SEM for ten replicate 2 x 10 m quadrats randomly located in each habitat. Refer to Table 1 for definitions of the habitat abbreviations.

Distribution of Spiders

Both *Geolycosa* species exhibited preferences and aversions for certain habitat types in Florida scrub (Fig. 3, Tables 7 and 8). In some cases, but not all, an explanation for the observed pattern can be given. As expected from Marshall's studies (1995a, 1997), *G. xera archboldi* was most abundant in sand pine scrub with rosemary (SSr), the most open, most xeric habitat characterized by extensive gaps of barren sand and scant leaf litter. *G. hubbelli* was most common in scrubby flatwoods with sand live oak (SFl) and in ridge sandhill with scrub hickory (RSh), habitats that have open canopies, moderately xeric soils, and bare patches in the herbaceous layer even in the prolonged absence of fire (Abrahamson *et al.*, 1984). On the other hand, these spiders are uncommon in temporary ponds (TP) and various flatwoods (FLp, FLg, FLw), which is not surprising because they have poorly drained soils and are often covered with standing water during the rainy season or longer. For example, in winter 1998 at the height of the El Niño event one could locate turrets of *G. hubbelli* in dry flatwoods, but close inspection revealed that most burrows in these sites were filled with water. This was the only year when *G. hubbelli* were often seen wandering in the scrub, perhaps flushed from their burrows by a rising water table.

The absence of *Geolycosa* in the ridge sandhill with turkey oak (RSt) habitat was investigated recently and found to be caused by the instability of its natural soil. The preponderance of coarse and medium size sand grains makes the RSt soil likely to fall down a slope under dry conditions. This results in rapid collapse of spider burrows even when the burrow entrance appears to remain intact (Halloran *et al.*, 2000). The other types of soils in other scrub habitats consist mostly of fine and very fine grained sands, so they are intrinsically more stable and suitable for burrowing by these spiders (Halloran *et al.*, 2000).

The apparent aversion of *Geolycosa* for the most widespread scrub habitat, scrubby flatwoods with inopina oak (SFi), was unexpected and its cause was enigmatic. As mentioned above, the various natural soils in the SFi are suitable for burrowing by wolf spiders. Moreover, soil moisture levels in the SFi year round are intermediate between the values in the SSr, preferred by *G. xera archboldi*, and those in the RSh and SFl, preferred by *G. hubbelli* (Abrahamson *et al.*, 1984). In addition, the SFi, SSr, RSh, and SFl are at the same elevation (40–45 m above mean sea level) and they are contiguous with one another in the scrub mosaic, so even though *Geolycosa* exhibit limited dispersal (~0.4 m/day) (Marshall, 1995b), the spiders should be able to colonize extensively the SFi habitat. Perhaps the inopina oaks, the predominant plant species in the SFi habitat, are antagonistic to burrowing wolf spiders. Inopina oaks quickly resprout from clonal rootstock after a fire and in the following spring they resume their annual cycle of shedding their leaves, which produces much leaf litter. Furthermore, leaves of inopina oaks are linear, not revolute like those of the sand live oak, so they form dense mats near the base of the plants. Therefore, within 8–10 years after a burn the dense thickets of shrubby inopina oaks and the associated mats of inopina oak litter may greatly reduce the gaps of open sand and microhabitats with a small amount of litter coverage that young *Geolycosa* prefer. This would render the SFi marginally suitable for *Geolycosa*. Research on the effects of fire and post-fire plant productivity on *Geolycosa* populations in the SFi is in progress.

Acknowledgements

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