25 September 2003
JOURNAL OF THE KANSAS ENTOMOLOGICAL SOCIETY
76(4), 2003, pp. 557-566

Burrowing Wolf Spiders, *Geolycosa* spp. (Araneae: Lycosidae): Gap Specialists in Fire-Maintained Florida Scrub

James E. Carrel
Division of Biological Sciences, 105 Tucker Hall,
University of Missouri-Columbia, Columbia, Missouri 65211-7400

ABSTRACT: Florida Scrub is a hotspot of biological diversity containing many endemic species such as burrowing wolf spiders (*Geolycosa* species), that are threatened by habitat destruction. This study investigated why two spicies, *G. xera archiboldi* (McCrone) and *G. hubbelli* Wallace, are significantly underrepresented in fire-maintained scrubby flatwoods, a widespread scrub habitat on the Lake Wales Ridge in south-central Florida. Palmettos resprouted within 1-2 weeks after a fire, then in the ensuing months oaks and lyonias dominated the vegetative community. Over the course of 10-11 years after a fire, woody shrubs grew logarithmically in height to form these dense thickets, causing the size of gaps in the vegetation to decline in a log-log fashion as a function of time-since-fire. Gaps in the shrub matrix shrank dramatically on average from about 20 m^2 at 0.5 mo postfire to only 0.01 m^2 at 120 mo postfire. In contrast, the average size of gaps harboring burrows of adult female spiders was found to be a species-specific trait, independent of time-since-fire: 1.0-1.2 m^2 for *G. xera archboldi* and 0.2-0.3 m^2 for *G. hubbelli*. Hence, gaps suitable for sustenance of both *Geolycosa* species became uncommon throughout scrubby flatwoods within 11 months after a fire.

KEY WORDS: *Geolycosa xera archboldi*, *Geolycosa hubbelli*, ecology, Florida scrub, fire, woody plant regeneration, gap dynamics, conservation biology

Introduction

Florida scrub is an ecosystem of high species endemism found only on ancient sandy ridges that form an archipelago of harsh habitat islands scattered across the peninsular portion of the state. Each parcel of Florida scrub consists of a mosaic of several vegetative communities dominated by woody shrubs and pine trees (Pinaceae) that are adapted to infertile soils, to seasonal drought, and to landscape-level fires that in prehistoric times were started by frequent lightning strikes (Abrahamson, 1984; Abrahamson *et al.*, 1984; Myers, 1990; Menges and Kohlfeldt, 1995; Abrahamson and Abrahamson, 1996; Menges, 1999). In general, rhizomes and roots of woody shrubs survive a burn and then soon resprout and grow clonally, so the characteristic physiognomy of each vegetative community in the scrub is quickly restored (Myers, 1990; Abrahamson and Abrahamson, 1996; Menges, 1999). Because Florida scrub has a highly restricted distribution and it contains a remarkably high density of rare, threatened, and endangered species, it is urgent that the unique species in these communities be studied so that appropriate land management practices can be instituted (Deyrup and Eisner, 1993; Kautz *et al.*, 1993; Eisner *et al.*, 1995; McCoy and Mushinsky, 1999; Menges, 1999).

Among the rare and possibly threatened arthropods endemic to Florida scrub are two syntopic species of burrowing wolf spiders, *Geolycosa xera archboldi* (McCrone, 1963) and *G. hubbelli* Wallace, 1942 (Araneae: Lycosidae) (Deyrup, 1989; Edwards, 1994; Marshall *et al.*, 2000). Recently it was shown that both species are significantly less common than expected in a widespread scrub habitat called scrubby flatwoods with inopina oak (*Quercus inopina* Ashe) (Fagaceae) (code name: SFi) (Carrel, 2003). It was suggested that after a fire, rapidly growing inopina oaks and other woody shrubs might quickly form

---

Corresponding author: Prof. James E. Carrel, 209 Tucker Hall, University of Missouri, Columbia, 65211-7400;
Telephone: 573-882-3037; FAX: 573-882-3037; e-mail: carrelj@missouri.edu

dense patches of vegetation, so that within less than a decade most gaps of open sand suitable for *Geolycosa* burrows would have been eliminated (Carrel, 2003). The purpose of this research was to determine temporal patterns in the regeneration of woody shrubs and changes in the size of gaps within the shrub matrix as the SFi recovered from burning and to contrast these results with data for the size of gaps occupied by adult females of the two *Geolycosa* species. If adult female spiders of each *Geolycosa* species were found to possess a gap of uniform size in the scrub matrix, presumably an indication of the minimal space needed for successful reproduction and recruitment, then one could use the postfire vegetation data to project when the SFi would become unsuitable for these spiders, resulting eventually in their decline.

Methods

STUDY AREA: The Archbold Biological Station (ABS) 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 628 ha portion of ABS used in this study (Tracts SW, 6, 7, and 18) is very flat: elevation ranged from 38 to 46 m above mean sea level. All field measurements were made in scrubby flatwoods with inopina oak (SFi), the most extensive vegetative association at ABS (~30% of the total hectarage). SFi is dominated by low shrubby oaks (principally *Q. inopina*, but to a lesser degree also *Q. geminata* Small, *Q. chapmanii* Sargent, *Q. myrtifolia* Willdenow, and *Q. minima* Small), palmettos (*Serenoa repens* Small and *Sabal etonia* Swingle) (Arecaceae), and shrubby lyonias (*Lyonia ferruginea* Nuttall, *L. fruticosa* Torrey, and *L. lucida* K. Koch) (Ericaceae). Other, less abundant woody species include gopher apple (*Licania michauxii* Prance) (Chrysobalanaceae), dwarf evergreen blueberry (*Vaccinium myrsinites* Lamarck) (Ericaceae), scrub holly (*Ilex opaca* var. *arenicola* Ashe) (Aquifoliaceae), silkbay (*Persea humilis* Nash) (Lauraceae), and palafoxia (*Palafoxia feayi* Gray) (Asteraceae). Using a detailed vegetation map for ABS developed by Abrahamson *et al.*, 1984, the boundaries of SFi habitat were readily located in the field.

BURN HISTORY: To manage prescribed burns at ABS and to restrict the spread of wildfires in the scrub, a series of 187 burn units bounded by primitive roads that served as fire breaks was established starting in 1977. In the preceding century landscape level fires were actively suppressed, especially after 1941 when ABS operated its own fire station (Main and Menges, 1997). A record of the date, area, intensity, and location of fires in each burn unit was compiled by ABS staff. In this study there were 48 burn units available. I selected 21 burn units with extensive SFi habitat that represented a chronoseries based on time-since-fire, ranging in age from 0.25 to 137 mo, for field measurements.

MEASUREMENTS OF VEGETATION AND GAPS: I established a 120 m long transect in each burn unit by overlaying the vegetation map with a grid, choosing a point at random within the polygon representing the SFi, and then randomly selecting a compass direction through which the transect was drawn. In the field I set the origin of each transect 10-15 m beyond the edge of the SFi, then I made vegetation measurements at 48 points separated by 2.5 m intervals. I marked a point by a thin vertical rod placed in the soil and measured the distance from the rod to the closest woody vegetation to the nearest 0.1 m. I also measured the height of the vegetation to the nearest 0.1 m and identified the plant species. To prevent bias, I systematically rotated the direction from the sample point to vegetation through the four cardinal compass directions (N, E, S, W ± 20°).

Gaps in the SFi are distinct because the edges of the shrub matrix are sharply defined (Menges and Hawkes, 1998). As in Menges and Hawkes (1998), Menges (1999), Young and Menges (1999), and Quintana-Ascencio and Menges (2000), I defined a gap as an area lacking living shrubs and shrub canopy. Operationally this meant the open area might consist of sand that was barren or covered with leaf litter and it might contain some herbs, lichens, standing dead ramets, or sprouting ramets less than 0.1 m in height.

I calculated the total number of woody plant species and the average height of woody vegetation that I encountered in each transect in the 21 burn units. Furthermore, assuming that natural gaps in the canopy were more-or-less round, as in Young and Menges (1999), I calculated the average area of a gap in a burn unit by letting the distance from a sample point to the edge of the vegetation be the radius of a circle. Subsequently, I determined the best-fit regression equation for the average height of the woody vegetation and the average area of gaps as a function of time-since-fire. Statistical tests of the residuals revealed that the data needed to be log-transformed to normalize the variation prior to regression analysis using SYSTAT (Wilkinson, 1989).

To assess floristic trends in regeneration of SFi, using a subset of the data described above, I contrasted the relative abundance of different taxa of woody vegetation in transects on 5 replicate burn units at 2 mo recovery in October 2002 with that on transects in 5 burn units approximately 60 times as old (age ranging from 118 to 137 mo postburn). I grouped species of woody vegetation in each burn unit into four taxonomic categories (palmettos, oaks, lyconias, and other species), and then I calculated the abundance (% of 48 samples/transect) of each category and converted the data by the arcsin transformation before I performed analysis by a 2-way ANOVA and the Tukey HSD test using SYSTAT(Wilkinson, 1989).

AREA OF GAPS USED BY ADULT FEMALE *GEOLYCOSA*: I hypothesized that the size of gaps in the SFi matrix occupied by adult females of each spider species might be a relatively invariant, species-specific trait. Carrel (2003) showed that the burrows of *G. xera archboldi* and *G. hubbelli* can be differentiated based on the architecture of the entrance, that open burrows are almost always occupied by a spider, and that burrows containing adult females are larger in diameter (≥7 and ≥11 mm, respectively) than those of immature conspecifics. In addition, *G. xera archboldi* females strongly prefer barren sand (0–10% coverage of leaf litter) whereas *G. hubbelli* females prefer sites with much leaf litter (60–80% coverage) (Carrel, 2003).

To determine whether the size of gaps inhabited by female *Geolycosa* might decline with time as the SFi habitat recovered from a burn, I located ten burrows of both species in each of three burn units that had recovered somewhat from a previous burn (19.5 mo postfire) and the same number in three burn units approximately six times as old (118–137 mo postfire). I established a series of transects at 10 m intervals parallel to those used previously in selected burn units and searched for female *Geolycosa* burrows along them, so the measures of spiders' gaps did not overlap vegetation measures. After I detected the burrow of a female spider, I measured the shortest distance across the gap and then, at a perpendicular angle, the long axis of the gap to the nearest 0.1 m. I calculated the size of the gaps (N = 120) using the formula for the area of an ellipse. I evaluated the relationship between gap area, spider species, and time since burn statistically by a 2-way ANOVA and the Tukey HSD test using SYSTAT (Wilkinson, 1989).

Results

POSTFIRE REGENERATION OF VEGETATION AND CLOSURE OF GAPS: Upon inspection of 21 burn units that differed in time-since-fire, the scrubby flatwoods with inopina oak (SFi) appeared to recover very rapidly after a burn. As shown in Fig. 1, species richness of woody shrubs increased in a logarithmic fashion with time-since-fire. Within 2 weeks many new leaves of the two species of

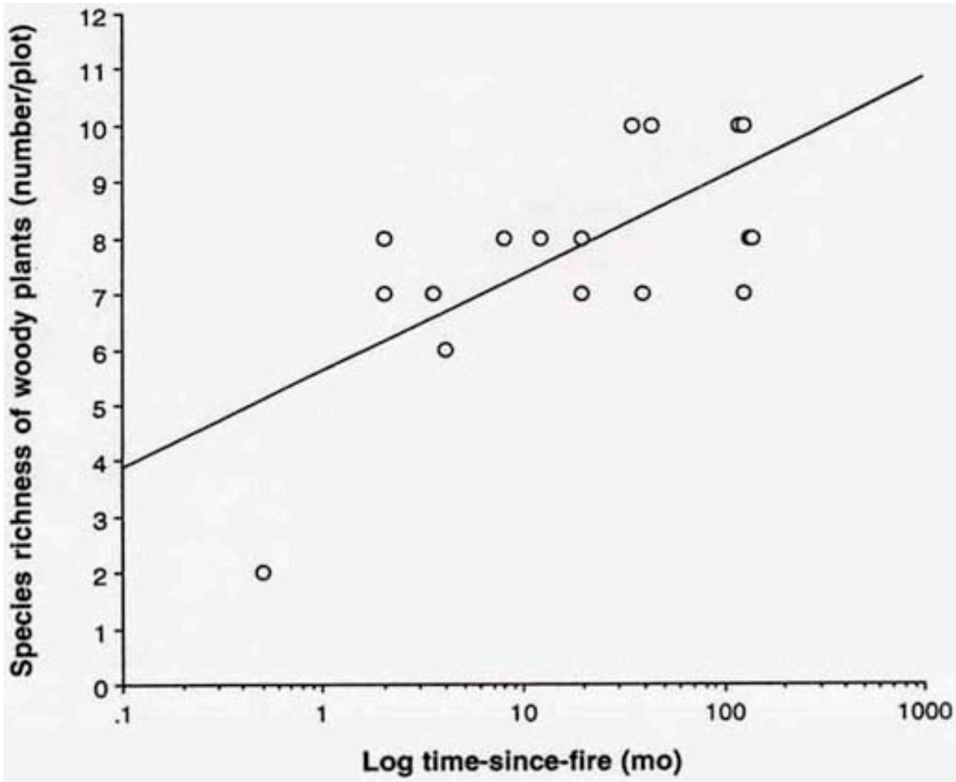

Fig 1. Total number of woody plant species in scrubby flatwoods with inopina habitat increased in a logarithmic fashion with time-since-fire (y = 5.6123 + 1.7414 (log x), R = 0.67, d.f. = 20; $P < 0.01$).

palmettos emerged and grew 0.1–0.2 m and some saw palmettos also produced inflorescences that were 0.2–0.3 m in length. At 2–4 mo postfire there were ramets of four to six additional woody species present, such as oaks, lyonias, gopher apple, and dwarf blueberry. The accumulation of new plant species declined greatly thereafter, so at 30-137 mo postfire there was a total of only seven to ten woody plant species growing commonly in a burn unit.

A subtle pattern of successional change in the community of woody plants forming the matrix of the SFi was revealed when the species composition in five recently burned (2 mo postfire) and five long unburned (~120 mo post fire) units was contrasted. Analysis of variance (Table 2) showed that there was a significant interaction between the age of burn and the abundance of different taxa of plants at a site.

Table 1. Analysis of variance (ANOVA) results showing the influence of main and interaction effects on the relative frequency of different woody plants in scrubby flatwoods. (N = 40, R^2 = 0.886, $P < 0.001$).

Source	Degrees of freedom	Mean square	F-value	P-value
Age of burn[a]	1	0.41	0.02	0.900
Plant group[b]	3	1814.31	72.26	<0.001*
Age of burn × Plant group	3	195.36	7.78	0.001*
Burn unit (covariate)[c]	1	0.09	<0.01	0.952
Error	31	25.11		

[a] The scrubby flatwoods were recently burned (2 mo) or long unburned (118-127 mo)
[b] The woody plants were placed into four groups: palmettos, oaks, lyonias, and other species.
[c] A total of ten burn units were studied, five of each age category.
* Significant ($P < 0.05$; 2-way ANOVA).

Table 2. Analysis of variance (ANOVA) results showing the influence of main and interaction effects on the area of gaps in the vegetation occupied by female *Geolycosa* spiders. (N = 120, R^2 = 0.434, P < 0.001).

Source	Degrees of freedom	Mean square	*F*-value	*P*-value
Age of burn[a]	1	<0.01	0.01	0.978
Spider species[b]	1	21.65	79.66	<0.001*
Age of burn × Spider species	1	0.52	1.90	0.171
Burn unit (covariate) [c]	1	0.39	1.43	0.235
Error	115	0.27		

[a] The scrubby flatwoods were recently burned (19.5 mo) or long unburned (118-127 mo).
[b] Two burrowing wolf spiders were studied: *G. xera archboldi* and *G. hubbelli*.
[c] Ten gaps around burrows of each spider species were sampled in six burn units, three of each age category.
* Significant (P < 0.05; 2-way ANOVA).

An explanation for this outcome is shown in Fig. 2. The frequency of oaks, the dominant taxon, did not change in the two types of burn units. Oaks accounted for 52.8–55.5% of the plants typically encountered in any transect survey. On the other hand, palmettos declined from an average of more than 21.4% to 9.4% whereas lyonias increased from an average of 14.4% to 30.9% of plant species

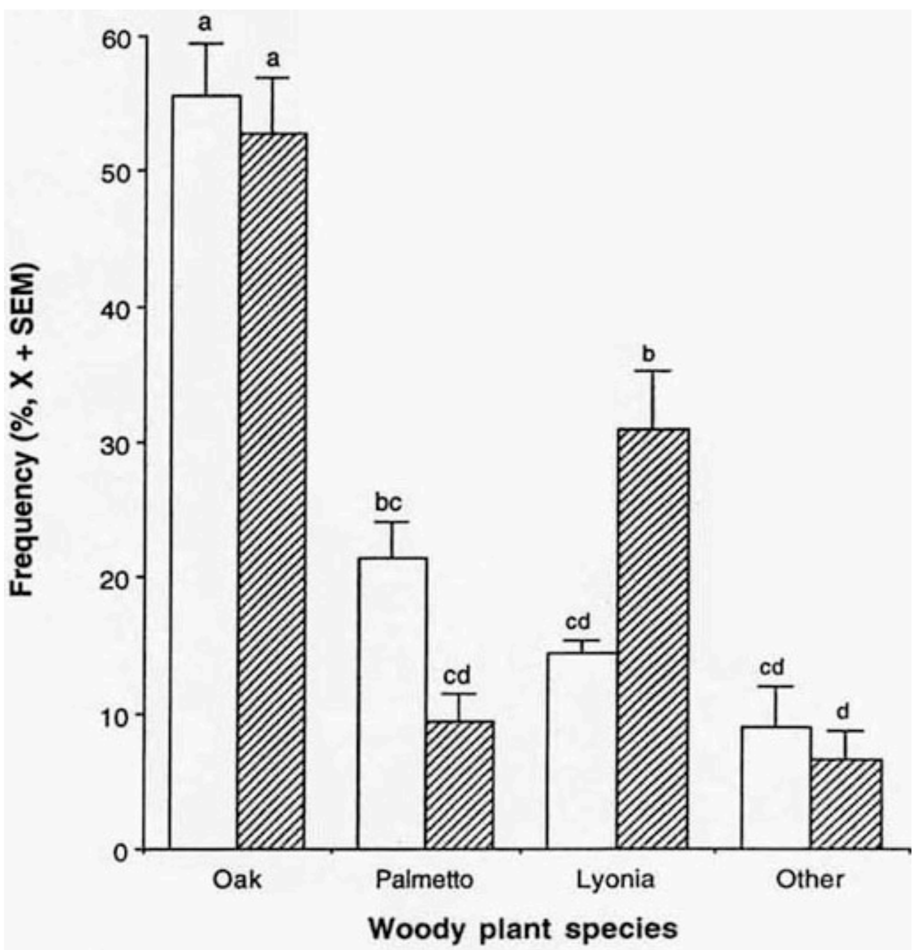

Fig 2. Contrast of the average frequencies of different taxa of woody shrubs in scrubby flatwoods with inopina oak habitat at 2 mo postfire (open bars) and at ~ 120 mo postfire (shaded bars). Data represent means + SEM for five replicates each with 48 samples in the two treatments. Bars sharing the same letter are not significantly different (P > 0.05) based on the Tukey HSD test using arcsin transformed data.

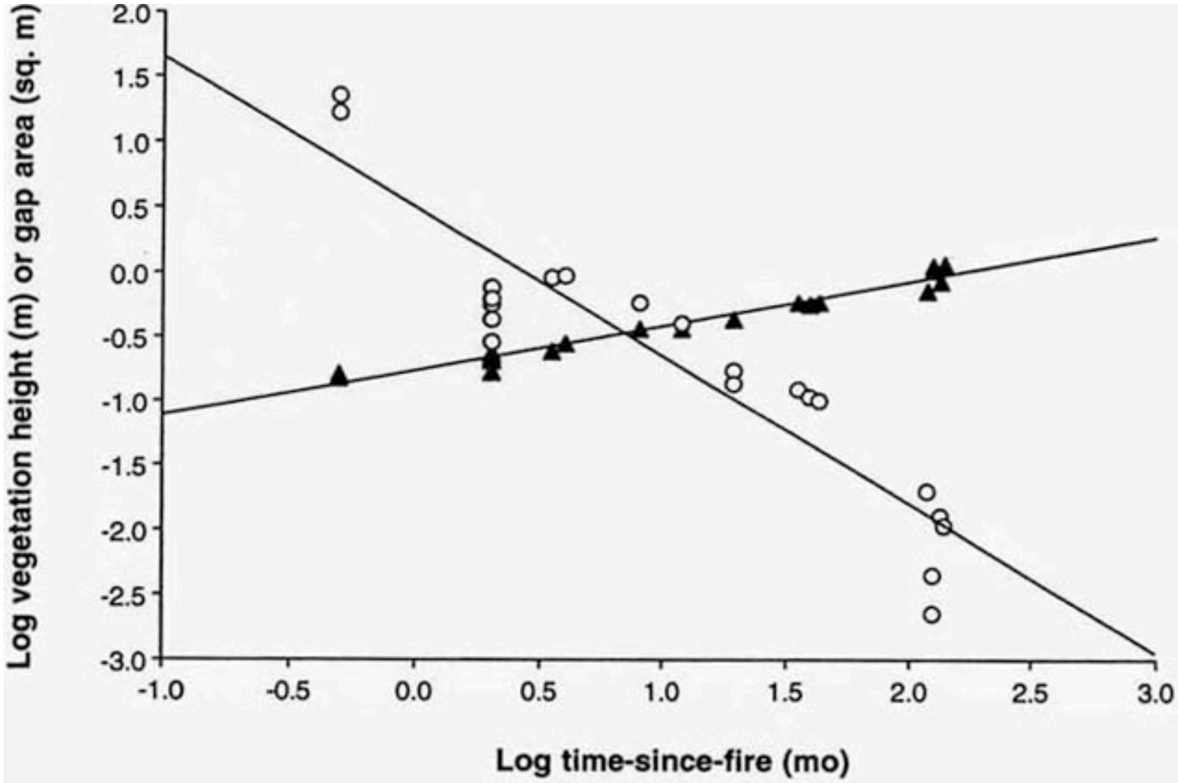

Fig. 3. Height of woody vegetation (solid triangles) increased and area of gaps (open circles) decreased as a log-log function of time-since-burn in scrubby flatwoods with inopina oak. Equations for the best-fit regression curves, as shown, are: height of vegetation, $y = -0.7738 + 0.3459x$, $R = 0.992$, d.f. = 20, $P < 0.001$; area of gaps, $y = 0.4997 - 1.1501x$, $R = 0.925$, d.f. = 20, $P < 0.001$

encountered. Other kinds of plants than those contained in the three taxa mentioned above were not different between the two age classes of scrubby flatwoods; they remained on average at 6.6–9.0% of woody plant species that were detected.

Field measurements in 21 burn units showed that the woody plants grew rapidly to an average of 0.35 m height during the first 12 mo after the SFi was burned, but thereafter, in the absence of fire, plant growth steadily diminished with time, so after about 120 mo average height of woody vegetation was only 1 m (Fig. 3). In a similar manner, gaps of open ground in the scrubby flatwoods declined dramatically from 20 m^2 at 0.5 mo to 0.2 m^2 on average at 12 mo after a burn, a decrease in mean area of approximately 99%, but thereafter the gaps decreased in size slowly with time (Fig. 3). These relationships proved to have a very statistically significant log-log relationship (Fig. 3).

AREA OF GAPS USED BY ADULT FEMALE *GEOLYCOSA*: Analysis of variance revealed that the area of open ground around a female spider's burrow (=gap size) was significantly associated with the spider's species identity (Table 2). However, time since the last burn event (= age of burn) and the burn unit in which a spider was found were not significant.

As shown in Fig. 4, the size of gaps harboring *G. xera archboldi* were typically about 1.0–1.2 m^2 and those utilized by *G. hubbelli* were commonly about 0.2–0.3 m^2. In five of six burn units, gaps used by *G. xera archboldi* were significantly greater than those used by *G. hubbelli*.

Discussion

POSTFIRE REGENERATION OF SCRUBBY FLATWOODS: In this study I identified 15 woody plant species in the 21 replicates of scrubby flatwoods with inopina oak (SFi) (see methods section). However,

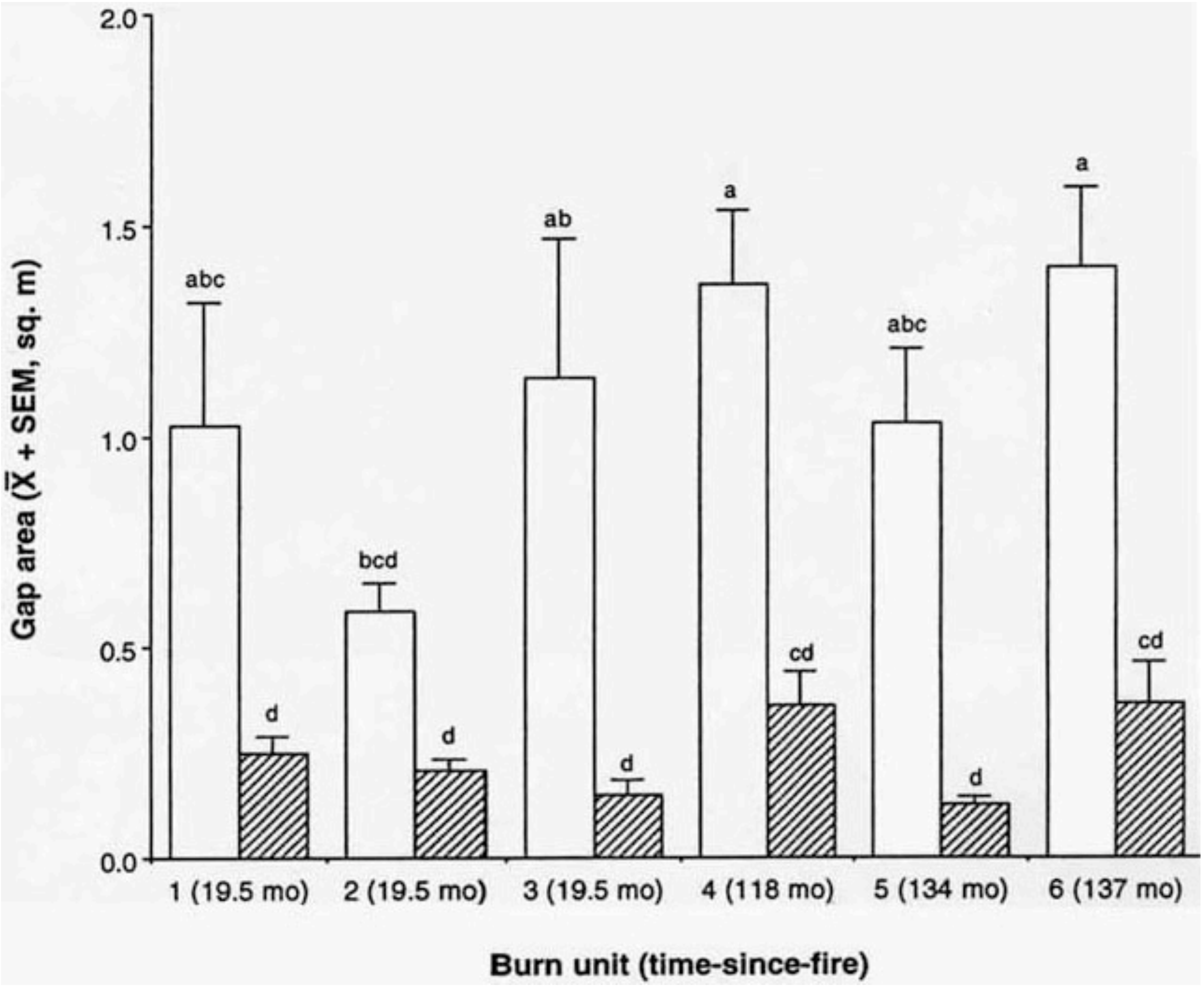

Fig. 4. Average area (m^2) of gaps occupied by *Geolycosa xera archboldi* (open bars) and *G. hubbelli* (shaded bars) in shrubby flatwoods with inopina oak habitat was a species specific trait, independent of time-since-fire. Data represent means + SEM for ten burrows for adult females of each species in three recently burned plots and three long unburned plots. Bars sharing the same letter are not significantly different ($P > 0.05$) based on the Tukey HSD test.

I found 10 or fewer species in any burn unit, even in ones having more than a decade for recovery from fire. A major reason for this discrepancy is that the shrubby oaks and lyonias overgrew and, in some instances, shaded out the more dwarfish species, such as gopher apple, dwarf evergreen blueberry, scrub holly, and the palmettos. Because I measured only the tallest ramets close to the 48 sample points in each burn unit, low growing shrubs tended to be counted in the SFi shortly after a burn but often they were not recorded in the SFi that was older. If I had adopted the quadrat sampling method used by Givens *et al.* (1984) to measure structural changes in the SFi as a function of time-since fire, then I certainly would have obtained a more complete floristic inventory. For example, unlike Givens *et al.* (1984), I did not report an slash pines (*Pinus elliottii* var. *densa* Little and Dorman) because, even though they were visible in many burn units, just by chance they never happened to be close to any of the 1008 sample points in my 21 transects. However, the results of the present study are very similar to those reported by Young and Menges (1999) for the vegetation recovery in a chronosequence of seven sites in the SFi, age 0–35 years postfire, that was performed previously at ABS. Of the fourteen woody species reported by Young and Menges (1999), twelve were common to both studies and two [dwarf huckleberry (*Gaylussacia dumosa* Torrey and Gray) (Ericaceae) and jointweed (*Polygonella polygama* Engelmann and Gray) (Polygonaceae)] were unique to their study. Hence, using Sørenson's index (Mueller-Dambois and Ellenberg, 1974), the coefficient of species similarity for the two studies was very high (83%).

Woody shrubs in the SFi grew at logarithmic rates, causing the vegetative community to regenerate within a few years, and thereafter it grew at ever more slowly but it did not stop. This is consistent with previously published reports that scrubby flatwoods recover in 1–4 years from fire (Abrahamson, 1984; young and Menges, 1999). Using the equation for growth in height of woody vegetation as a function of time-since-fire (Fig. 3), I projected that the average height of vegetation in SFi habitats at ABS that had not been burned for 40 and 50 years would be 1.42 and 1.54 m, respectively. Previous work of Givens *et al.* (1984) reported that the height of shrubs and trees in burn units of these ages was considerably smaller (median values approximately 0.9 and 1.0 m, respectively). As explained previously, the difference between the outcomes of the two studies likely is an artifact generated by employment of different field techniques.

GAP DYNAMICS OF BURROWING WOLF SPIDERS: Burrowing wolf spiders (*Geolycosa* spp.) in Florida scrub spend most of their lives hidden in their burrows, so the burrow serves as a refuge and the open area surrounding it functions both as a territory and as a foraging arena (Emerton, 1912; Wallace, 1942; McCrone, 1963; Marshall, 1995b, 1996, 1997, 1999; Marshall *et al*., 2000). Abandonment of burrows is common in young *Geolycosa* but it is infrequent in more mature individuals (Marshall, 1995a; Carrel, 2003), suggesting that immature spiders may actively assess the quality of a gap in terms of soil properties, gap openness, prey availability, and proximity of conspecifics. Presumably if a gap proves to be a low quality, then the spider disperses a short distance (at most a few meters), builds another burrow, and repeats the evaluation process. Hence, the gaps occupied by adult females probably represent the outcome of a long, iterative process of microsite evaluation (adult males leave their burrows and wander in search of mates). It is no wonder then that the burrows of large *Geolycosa* are considered to be semi-permanent (Emerton, 1912; Wallace, 1942; McCrone, 1963).

I found that gaps occupied by *G. xera archboldi* females were about four times larger in area than those used by *G. hubbelli* (Fig. 4). This is consistent with the openness of the vegetative communities these spiders naturally prefer in Florida scrub. Recently Carrel (2003) showed that *G. xera archboldi* prefers the most open habitat at ABS (sand pine scrub with rosemary (SSr)), whereas *G. hubbelli* prefers two communities having open canopies and bare patches of soil even in the prolonged absence of fire (ridge sandhill with scrub hickory (RSh) and scrubby flatwoods with sand live oak (SSo)).

Using the regression equation for gap size in the SFi as a function of time-since-fire in Fig. 3, I calculated that large gaps suitable for *G. xera archboldi* females (1.0–1.2 m^2) would become uncommon in only 2.3–2.7 mo postfire. Likewise, small patches typically occupied by *G. hubbelli* females (0.2–0.3 m^2) would disappear in 7.7–11.0 mo as the scrubby matrix regenerated. These results strongly suggest that the SFi at ABS cannot sustain dense populations of both *Geolycosa* species within a few years postfire simply because there are not many suitable sites available for the spiders. In a sense, the rather sessile, recondite burrowing wolf spiders are faced with the same problems as the seeds of rare herbaceous plant species that are narrowly endemic to Florida scrub: all require persistent openings between shrubs in order to grow and successfully reproduce (Menges and Kimmich, 1996; Menges and Hawkes, 1998; Quintana-Ascencio and Menges, 1996, 2000; Quintana-Ascencio *et al*., 1998; Menges, 1999).

Based on the results of this study, one might recommend that the SFi be managed by controlling the fire return interval to promote formation of gaps suitable for *Geolycosa*. The problem is that the creation of gaps in Florida scrub has been little studied (Menges and Hawkes, 1998). Historical data indicate that the SFi is adapted to a modal fire return interval ranging from 6 to 9 years (Main and Menges, 1997), so one might advocate this as a best practice. However, models for vegetation dynamics in Florida scrub suggest that frequent fires (1-10 year intervals) may cause some of the xeric communities, such as SSr and SSo, that naturally have many gaps and large populations of *Geolycosa*, to be replaced by SFi (Myers, 1985; Menges and Hawkes, 1998; Menges, 1999; Carrel, 2003). Hence, there does not seem to be a single burning regime that is best for burrowing wolf spiders in the mosaic of scrub communities. If the 187 burn units at ABS are managed in such a fashion that the fire return interval for each is systematically varied, as proposed by Main and Menges (1997), then after several decades one might be able to determine the tradeoffs for both *Geolycosa* species in the SFi and other vegetative communities.

Acknowledgements

I thank the staff of the Archbold Biological Station for providing research facilities and Jan C. Weaver for technical assistance. Funding for this work came in part from a grant from the Development Fund at the University of Missouri.

Literature Cited

Abrahamson, W. G. 1984. Post-Fire recovery of Florida Lake Wales Ridge vegetation. American Journal of Botany 71:9–21.

Abrahamson, W. G., and C. R. Abrahamson. 1996. Effects of fire on long-unburned Florida uplands. Journal of Vegetation Science 7:565–574.

Abrahamson, W. G., A. F. Johnson, J. N. Layne, and P.A. Peroni. 1984. Vegetation of the Archbold Biological Station, Florida: an example of the southern Lake Wales Ridge. Florida Scientist 47:209–250.

Carrel, J. E. 2003. Ecology of two burrowing wolf spiders (Araneae: Lycosidae) syntopic in Florida scrub: burrow/body size relationships and habitat preferences. Journal of the Kansas Entomological Society 76:16–30.

Deyrup, M. A. 1989. Arthropods endemic to Florida scrub. Florida Scientist 52:125–128.

Deyrup, M., and T. Eisner. 1993. Last stand in the sand. Natural history 102(12):42–47.

Eisner, T., J. Lubchenco, E. O. Wilson, D. S. Wilcove, and M. J. Bean. 1995. Building a scientifically sound policy for protecting endangered species. Science 269:1231–1232.

Edwards, G. B. 1994. McCrone's burrowing wolf spider. *In* M. Deyrup and R. Franz (eds.). Rare and Endangered Biota of Florida, Vol. 4, Invertebrates, pp. 232–233. University Presses of Florida, Gainesville, FL.

Emerton, J. J. 1912. Four Burrowing *Lycosa* (*Geolycosa* Montag, *Scaptocosa* Banks) including one new species. Psyche 19:25–36.

Givens, K. T., J. N. Layne, W. G. Abrahamson, and S. C. White-Schuler. 1984. Structural changes and successional relationships of five Florida Lake Wales Ridge plant communities. Bulletin of the Torrey Botanical Club 111:8–18.

Kautz, R. S., D. T. Gilbert, and G. M. Mauldin. 1993. Vegetative cover in Florida based on 1985–89 Landsat thematic mapper imagery. Florida Scientist 56:135–154.

Main, K. N., and E. S. Menges. 1997. Station management plan. Archbold Biological Station Land Management Publication 97–1. 104 pp.

Marshall, S. D. 1995a. Natural history, activity patterns and relocation rates of a burrowing wolf spider: *Geolycosa xera archboldi* McCrone (Araneae, Lycosidae). Journal of Arachnology 23:65–70.

Marshall, S. D. 1995b. Mechanisms of the formation of territorial aggregations of the burrowing wolf spider *Geolycosa xera archboldi* McCrone (Araneae, Lycosidae). Journal of Arachnology 23:145–150.

Marshall, S. D. 1996. Evidence for territorial behaviour in a burrowing wolf spider. Ethology 102:32–39.

Marshall, S. D. 1997. The ecological determinants of space use by a burrowing wolf spider in a xeric shrubland ecosystem. Journal of Arid Environments 37:379–393.

Marshall, S. D. 1999. Neighborhood effects within territorial aggregations of the burrowing wolf spider *Geolycosa xera archboldi* McCrone (Araneae: Lycosidae). Canadian Journal of Zoology 77:1006–1012.

Marshall, S. D., W. R. Hoeh, and M.A. Deyrup. 2000. Biogeography and conservation biology of Florida's *Geolycosa* wolf spiders: threatened spiders in endangered ecosystems. Journal of Insect Conservation 4:11–21.

McCoy, E. D., and H. R. Mushinsky. 1999. Habitat fragmentation and the abundances of vertebrates in the Florida scrub. Ecology 80:2526–2538.

McCrone, J. D. 1963. Taxonomic status and evolutionary history of the *Geolycosa pikei* complex in the southeastern United States (Araneae, Lycosidae). American Midland Naturalist 70:47–73.

Menges, E. S. 1999. Ecology and conservation of Florida scrub. *In* R. C. Anderson, J. S. Fralish, and J. M. Baskin (eds.). Savannas, Barrens, and Rock Outcrop Plant Communities of North America, pp. 7–22. Cambridge University Press, Cambridge, UK.

Menges, E. S., and C. V. Hawkes. 1998. Interactive effects of fire and microhabitat on plants of Florida scrub. Ecological Applications 8:935–946.

Menges, E. S., and J. Kimmich. 1996. Microhabitat and time-since-fire: effects on demography of *Eryngium cuneifolium* (Apiaceae), a Florida scrub endemic plant. American Journal of Botany 83:185–191.

Menges, E. S., and N. Kohfeldt. 1995. Life history strategies of Florida scrub plants in relation to fire. Bulletin of the Torrey Botanical Club 122:282–297.

Mueller-Dombois, D., and H. Ellenberg. 1974. Aims and Methods of Vegetation Ecology. J.Wiley and Sons, NY. 547 pp.

Myers, R. L. 1985. Fire and the dynamic relationship between Florida sandhill and sand pine scrub vegetation. Bulletin of the Torrey Botanical Club 112:241–252.

Myers, R. L. 1990. Scrub and high pine. *In* R. L. Myers and J. J. Ewel (eds.). Ecosystems of Florida, pp. 150–193. University of Central Florida Press, Orlando, FL.

Quintana-Ascencio, P., and E. S. Menges. 1996. Inferring metapopulation dynamics from patch-level incidence of Florida scrub plants. Conservation Biology 10:1210–1219.

Quintana-Ascencio, P., and E. S. Menges. 2000. Competitive abilities of three narrowly endemic plant species in experimental neighborhoods along a fire gradient. American Journal of Botany 87:690–699.

Quintana-Ascencio, P., R. W. Dolan, and E. S. Menges. 1998. *Hypericum cumulicola* demography in unoccupied and occupied Florida scrub patches with different time-since fire. Journal of Ecology 86:640–651.

Wallace, H. K. 1942. A revision of the burrowing spiders of the genus *Geolycosa* (Araneae, Lycosidae). American Midland Naturalist 27:1–62.

Wilkinson, L. 1989. SYSTAT: The System for Statistics. SYSTAT, Incorporated, Evanston, IL. 638 pp.

Young, C. C., and E. S. Menges. 1999. Postfire gap-phase regeneration in scrubby flatwoods on the Lake Wales Ridge. Florida Scientist 62:1–12.