

## Habitat associations of the web-building wolf spiders *Sosippus floridanus* and *Sosippus placidus* (Lycosidae: Sosippinae): a widespread generalist versus an endemic specialist

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**Abstract.** Habitat associations of two species of congeneric web-building wolf spiders were examined in their zone of syntopy on the Lake Wales Ridge in Florida. The species differed in use of all of the habitat variables measured. The geographically widespread species, *Sosippus floridanus* Simon, 1898, associated with habitat features typical of scrubby flatwoods and human disturbed areas, which are found throughout the Florida peninsula. The endemic species, *S. placidus* Brady, 1972, associated with a scrub oak habitat that is restricted to the Lake Wales Ridge. Biogeographic implications of these differences are discussed.

**Keywords:** Florida scrub, biogeography, web-site selection, syntopic

Lycosidae is a large family of spiders (2421 species, 124 genera) distributed world-wide in a great range of habitats (World Spider Catalog 2018). The vast majority are vagrant hunters, either lying in wait for or wandering in search of prey. Some species are sedentary, building more-or-less permanent burrows from which they ambush passing prey, and only a minority of species build prey capture webs (Murphy et al. 2006). Wolf spiders in the subfamily Sosippinae are all obligate web-builders (Brady 2007). The genus *Sosippus* Simon, 1888 builds webs that exhibit a remarkable resemblance to webs of the funnel-web building family Agelenidae. In fact, there was some initial speculation that *Sosippus* might represent a transitional genus between the Agelenidae and Lycosidae (Brady 1972), however more recent analysis does not support that position (Griswold 1993; Griswold et al. 1999). The current view is that while it is not monophyletic, sheet-web building is an ancestral trait in lycosids, which once lost is unlikely to have been regained (Murphy et al. 2006).

The geographic distribution of *Sosippus* ranges from the southern United States, through Mexico and Central America to Costa Rica (Brady 1962, 2007). There are currently ten described species. The only species that have been studied in any depth are the four that occur on the Florida Peninsula (Brady 1972, 2007). The geographic distribution of Florida *Sosippus* is consistent with an evolutionary history of relict southeastern expansion during glacial periods, with speciation and isolation on islands during interglacial periods (Marshall et al. 2000). Of interest to our study is the isolation of areas of habitat defined as Florida scrub. During interglacial periods when sea levels rose, the higher areas of Florida became isolated as a series of islands (Deyrup 1989; Myers 1990; Webb 1990). These islands accumulated great depths of sand around their margins. Isolated from one another these islands each evolved unique flora and fauna. After sea level dropped, these deep piles of sand were scattered down the central area of the Florida peninsula. Even though they currently receive the same abundant rainfall typical of Florida in general, they retain their dry adapted plants and animals because any rainfall they receive rapidly drains from the deep sandy soils. Thus, each of these ancient islands possess plants and animals

found nowhere else in the world (Deyrup 1989; Marshall et al. 2000).

The distribution of *Sosippus placidus* Brady, 1972 is restricted to one of these habitat islands, the Lake Wales Ridge in south central Florida (Brady 1972, 2007). Its distribution is so restricted, primarily to Archbold Biological Station (ABS) and a few scrub remnants near Lake Placid, Florida (hence, the species name), that it was listed as endangered by the Florida Committee on Rare and Endangered Plants and Animals (Edwards 1994). In contrast, *Sosippus floridanus* Simon, 1898 co-occurs with *S. placidus* at ABS but also extends from southern Georgia, through the Florida peninsula to the Florida Keys (Brady 1972, 2007). Brady (1972, 2007) has suggested that the historical Pleistocene isolation led to subsequent reduction in genetic variability, limited dispersal abilities and ecological specialization for xeric conditions by *S. placidus*. The widespread distribution of *S. floridanus* may be due to originally having had a more northern distribution, escaping isolation on the xeric Pleistocene islands, and then spreading down the Florida peninsula after the interglacial. In this study, we examine these hypotheses by comparing web site characteristics of these two species at ABS, where they are syntopic. We predicted that *S. placidus* would show scrub-specific habitat associations whereas *S. floridanus* would exhibit a more generalized set of web site characteristics reflecting a lack of ecological specialization.

### METHODS

Research was conducted at Archbold Biological Station, an independent ecological research facility located in Venus, Florida, between May–June 2002. Visual search was used to locate webs which are visible in the early morning when covered with dew. The field station has an extensive network of fire roads which were used to access the scrub. A total of ten different surveys (on ten different days) were conducted. When a web was located, a meter stick was positioned above it, parallel to the direction of the funnel and centered on it at the 50-cm mark. The species was identified by flushing the spider out of the funnel onto the web. The two species are visually

Table 1.—Standardized discriminant function coefficients predicting the placement of *S. placidus* webs ( $n = 149$ ) versus *S. floridanus* webs ( $n = 112$ ) ranked using  $F$  scores. Due to lack of normality, the significance level is based on Mann-Whitney U tests. Pooled within-groups correlations between discriminating variable and standardized canonical discriminant functions show that only grass (negative value) predicts *S. floridanus* websites whereas all other variables (positive values) predict *S. placidus* websites.

Habitat variable	$F$	$P$	Canonical correlation coefficient
Pine litter	124.07	<0.0001	0.594
Grass	79.80	<0.0001	-0.476
Cactus	31.58	0.0005	0.192
Sand	25.76	<0.0001	0.271
Leaf litter	24.85	<0.0001	0.266
Gopher apple	18.60	<0.0001	0.230
Vine	16.90	<0.0001	0.219
Lichen	14.61	<0.0001	0.204

quite distinct from each other (*S. floridanus*: carapace with distinct white median stripe, legs brownish-yellow; *S. placidus*: carapace with broad marginal stripes of pale orange, legs with alternating light and dark stripes; Brady 2007). We used a line-intercept method to record habitat variables (Riechert 1976; Marshall & Martin 2011). The presence of plant species and substrate characteristics was recorded along the meter stick at 10 cm intervals. Substrate features included deciduous leaf litter, pine litter, and no litter (open sand). Vegetation included grass (species undetermined), cactus (*Opuntia humifusa*), gopher apple (*Licania michauxii*), vines (*Smilax auriculata* and *Vitis rotundifolia*) and lichen (*Cladonia* spp.). Once a web was scored, it was marked with a flag to avoid re-census. Two sets of transects were conducted. In one set the characteristics of *S. placidus* webs ( $n = 149$ ) were compared to those of *S. floridanus* ( $n = 112$ ). To determine if any particular feature of

scrub characterized *S. placidus* webs, a separate set of transects compared a web transect ( $n = 39$ ) to an additional random transect ( $n = 39$ ) that was taken a regular distance away. This random transect was chosen by taking a number of steps directly away from the end of the transect as determined by pairs of numbers from a random number table. The first number was the number of steps away, and the second number then determined a number of steps to the right (if the digit was even) or to the left (if the digit was odd) of the first endpoint. Discriminant analysis was used to determine habitat association (JMP ver. 13, SAS Institute Inc.) using site (*S. placidus* web, *S. floridanus* web, or random site) and habitat variable as factors. Since none of the variables were normally distributed, univariate non-parametric tests (Mann-Whitney U) were conducted on each variable rather than  $F$  statistics (Riechert 1976; Marshall 1997). Voucher specimens have been deposited at the Denver Museum of Nature and Science.

RESULTS

**Comparison of *S. placidus* and *S. floridanus* websites.**—A total of 149 one meter transects centered on *S. placidus* websites and 112 centered on *S. floridanus* websites were completed. There were clear differences in the websites of *S. placidus* and *S. floridanus* with respect to all of the habitat variables measured (Table 1, Fig. 1). Of all of the variables tested, discriminant analysis shows that only grass was strongly associated with *S. floridanus* websites, whereas pine litter and open sand were strongly associated with *S. placidus* websites (Table 1). We compared the average number of 10 cm transect intervals occupied by each habitat variable on the 1m transects through *S. floridanus* ( $n = 112$ ) and *S. placidus* webs ( $n = 149$ ). We found that *S. floridanus* was primarily associated with grass and *S. placidus* was primarily associated with pine litter (Fig. 1).

**Comparison of *S. placidus* websites and random sites.**—Comparing transects through *S. placidus* webs ( $n = 39$ ) with

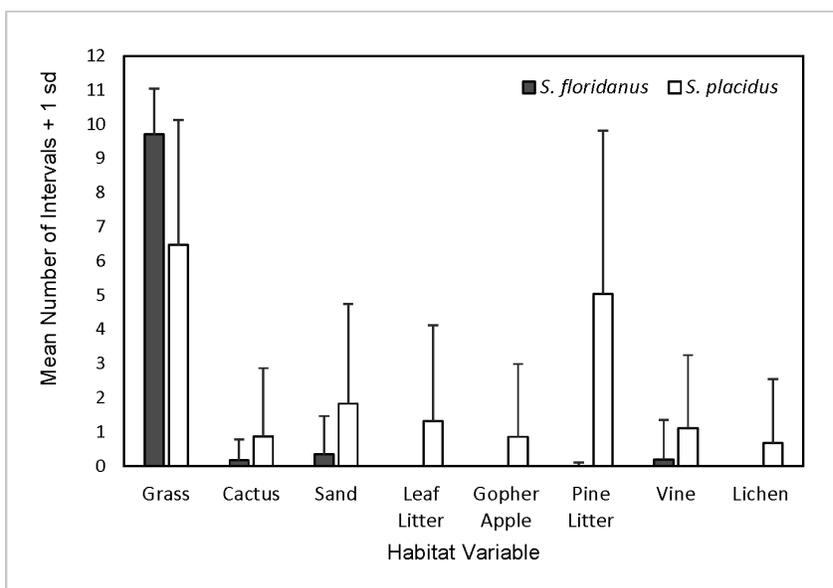


Figure 1.—Average number of 10 cm intervals per meter (+/- 1 s.d.) occupied by various habitat variables on transects through *S. floridanus* ( $n = 112$ ) and *S. placidus* webs ( $n = 149$ ).

Table 2.—Standardized discriminant function coefficients predicting the placement of *S. placidus* websites ( $n = 39$ ) compared to random sites ( $n = 39$ ), ranked using  $F$  scores. Due to lack of normality, the significance level is based on Mann-Whitney U tests. Pooled within-groups correlations between discriminating variable and standardized canonical discriminant functions show that only sand, lichen and gopher apple (negative values) predict random sites whereas all other variables (positive values) predict *S. placidus* websites.

Habitat variable	$F$	$P$	Canonical correlation coefficient
Cactus	22.22	<0.0001	0.734
Sand	5.11	0.0758	-0.356
Pine litter	2.15	0.1601	0.231
Vine	1.19	0.2190	0.172
Lichen	0.90	0.1447	-0.150
Leaf litter	0.52	0.5405	0.114
Grass	0.46	0.4697	0.107
Gopher apple	0.39	0.5995	-0.099

transects through random sites ( $n = 39$ ), the only significant difference was in the presence of the cactus *O. humifusa* at *S. placidus* websites (Table 2; Fig. 2). Discriminant analysis found that *O. humifusa* was the primary predictor of *S. placidus* websites whereas open sand was more prevalent at random sites (Table 2).

## DISCUSSION

This is the first in-depth examination of habitat associations of *Sosippus*. Anecdotal observations have recorded *S. floridanus* as occurring in pine flatwoods (Muma 1973) and high pine/palmetto (Brady 2007) plant communities, both of which are common to the entire Florida peninsula. The habitats at ABS are a mosaic of different plant communities including scrubby flatwoods and sand pine scrub (Abrahamson et al. 1984). The areas where we found *S. floridanus* are defined as scrubby flatwoods. Abrahamson et al. (1984)

divides scrubby flatwoods into three phases: inopina oak (*Quercus inopina*), sand live oak (*Q. geminata*) and human-introduced Bahia grass. As reflected by the transect data, *S. floridanus* were largely associated with grass (Table 1, Fig. 1). Webs were found primarily in disturbed areas around the station grounds and along the margins of fire roads and fences, areas in which we never found *S. placidus*.

In contrast, *S. placidus* webs were located primarily in habitat defined as sand pine scrub/oak which is dominated by scrub oaks (*Quercus* spp.) and sand pine (*Pinus clausa*) (Abrahamson et al. 1984). Much of this habitat is located in some of the higher elevation areas of ABS, with very well drained soil and typically xeric adapted plants, such as the cactus *O. humifusa*. In the transects comparing *S. placidus* and *S. floridanus* websites, 24% of *S. placidus* webs were associated with *O. humifusa*; only 8% of *S. floridanus* websites were. In the comparison of *S. placidus* websites with random transects, 54% of *S. placidus* webs were associated with *O. humifusa*, while only 2% of random transects encountered it. The adaptive nature of this association becomes very clear when one tries to collect *S. placidus*. When associated with cactus, the funnel entrance is usually located at the base of the plant, making it very difficult for collectors, or more importantly, predators, to gain access to the spider without injury. Other scrub specific habitat variables (Myers 1990) associated with the presence of *S. placidus* but not with *S. floridanus* include gopher apple (*L. michauxii*), lichens (*Cladonia* spp) and lack of litter/open sand (Table 2).

This habitat separation of syntopic congeners is very similar to what has been found in studies of Florida species of the genus *Geolycosa* Montgomery, 1904 (Araneae: Lycosidae). Like *S. placidus*, *Geolycosa xera archboldi* McCrone, 1963 is found only in Highlands County (Marshall et al. 2000). *Geolycosa hubbelli* Wallace, 1942 is syntopic with *G. x. archboldi* in Highlands County, but similar to *S. floridanus*, has a wider distribution (Marshall et al. 2000). Comparisons of burrow site selection of these two species found that *G. x. archboldi* at ABS is strongly associated with xeric scrub habitats, similar to *S. placidus* (Marshall 1997; Marshall et al. 2000; Carrel 2003; Marshall & Martin 2011). Similar to *S.*

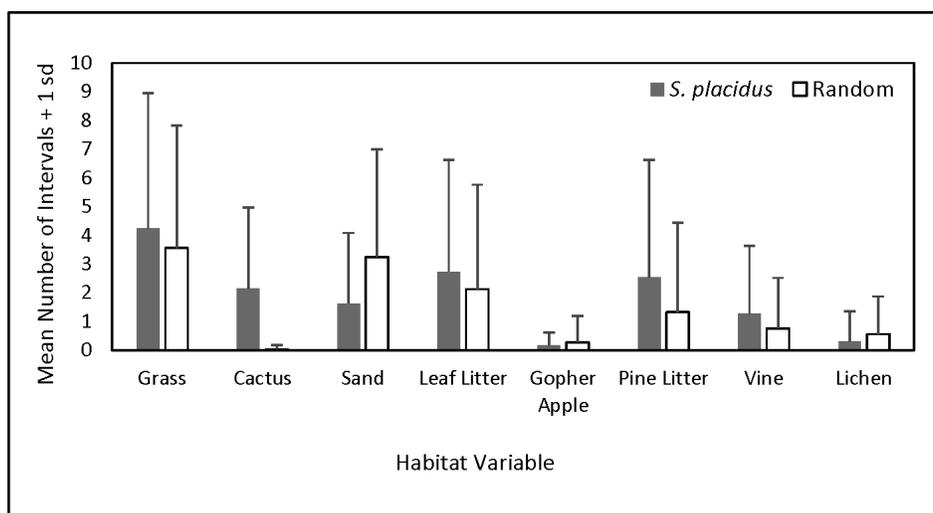


Figure 2.—Average number of 10 cm intervals per meter ( $\pm 1$  s.d.) occupied by various habitat variables on transects through *S. placidus* websites ( $n = 39$ ) and randomly selected sites ( $n = 39$ ).

*floridanus*, *G. hubbelli* has a more generalized set of burrow site characteristics (Marshall et al. 2000; Marshall & Martin 2011).

Another similarity between the scrub endemics *S. placidus* and *G. x. archboldi* is limited dispersal ability. When *G. x. archboldi* spiderlings leave the maternal burrow, they disperse a very short distance before digging their own burrows (on average 55 cm), and if they relocate burrow sites again, move a short distance (on average 43 cm; Marshall 1997). *Sosippus placidus* is unique among wolf spiders in that the female exhibits extensive maternal care that qualifies as subsocial behavior. Brach (1976) conducted field and laboratory studies of this behavior at ABS (it should be noted, that when Brach published this work he was unaware that the spiders had been renamed by Brady (1972) and so he describes them as *S. floridanus*). He found that the young stayed in the maternal web for up to 5 months, subsequently dispersing into the immediate vicinity or building their own webs at the edge of the maternal web. The female captured and paralyzed prey for the young and fed very little during this period. (Brach 1976; Hodge, personal observation). Observations of *S. janus* Brady, 1972, which also has a very restricted ridge-associated distribution, suggests they may also exhibit subsocial behavior (Brady 2007; Hodge, personal observation). To date, no observations on maternal care and dispersal of *S. floridanus* exist. Many scrub endemics exhibit limited dispersal, presumably because they are adapted to the xeric conditions of scrub “islands” (Deyrup 1990). Our observations support the speculation of Brady (2007) that geographic isolation on Pleistocene islands resulted in the ecological specialization and limited dispersal behavior of *S. placidus*.

We initially hypothesized that the biogeographic distribution of *S. placidus* and *S. floridanus* reflected isolation of *S. placidus* to xeric dune systems during interglacial periods, with dispersal of *S. floridanus* down the peninsula during subsequent wetter and cooler periods. Based on morphological features Brady suggests that *S. floridanus* may be the most recently derived species (Brady 2007). Molecular work is currently underway to shed further light on the phylogenetic history of the Floridanus group of *Sosippus* (Hodge & Cushing, in progress). Still true, even a decade after Alan Brady wrote these words “The study of *Sosippus*, involving its phylogenetic relationships to other Lycosidae, its ecological and geographical distribution pattern, and its subsocial behavior, continues to raise many interesting questions” (Brady 2007, p. 55).

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#### LITERATURE CITED

- Abrahamson, W.G., A.F. Johnson, J.N. Layne & P.A. Peroni. 1984. Vegetation of the Archbold Biological Station, Florida: an

- example of the southern Lake Wales Ridge. *Florida Scientist* 47:209–250.
- Brach, V. 1976. Subsocial behavior in the funnel web spider *Sosippus floridanus* (Araneae, Lycosidae). *Florida Entomologist* 59:225–229.
- Brady, A.R. 1962. The spider genus *Sosippus* in North America, Mexico, and Central America (Araneae, Lycosidae). *Psyche* 69:129–164.
- Brady, A.R. 1972. Geographic variation and speciation in the *Sosippus floridanus* species group (Araneae: Lycosidae). *Psyche* 79:27–48.
- Brady, A.R. 2007. *Sosippus* revisited: review of a web-building wolf spider genus from the Americas (Araneae: Lycosidae). *Journal of Arachnology* 35:54–83.
- 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* 52:254–270.
- Deyrup, M.A. 1990. Arthropod footprints in the sands of time. *Florida Entomologist* 73:529–538.
- Edwards, G.B. 1994. Lake Placid funnel wolf spider, *Sosippus placidus* Brady. Pp. 230–231. *In* Rare and Endangered Biota of Florida, Volume IV, Invertebrates. (M.A. Deyrup, R. Franz, eds.). University Press of Florida, Gainesville, FL.
- Griswold, C.E. 1993. Investigations into the phylogeny of the Lycosid spiders and their kin (Arachnida: Araneae: Lycosidae). *Smithsonian Contributions to Zoology* 539:1–48.
- Griswold, C.E., J.A. Coddington, N.I. Platnick & R.R. Forster. 1999. Towards a phylogeny of entelegyne spiders (Araneae, Araneomorphae, Entelegynae). *Journal of Arachnology* 27:53–56.
- 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. & K.A. Martin. 2011. Correlated morphological, ecological and behavioral aspects of the microhabitat associations of *Geolycosa* wolf spiders of Florida (Araneae: Lycosidae). *Southeastern Naturalist* 10:357–364.
- Marshall, S.D., W.R. Hoeh & 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.
- Muma, M.H. 1973. Comparison of ground surface spiders in four central Florida ecosystems. *Florida Entomologist* 56:173–196.
- Murphy, N.P., V.W. Framenau, S.C. Donnellan, M.S. Harvey, Y. Park & A.D. Austin. 2006. Phylogenetic reconstruction of the wolf spiders (Araneae: Lycosidae) using sequences from the *12S rRNA*, *28S rRNA*, and *NADH1* genes: implications for classification, biogeography, and the evolution of web building behavior. *Molecular Phylogenetics and Evolution* 38:583–602.
- Myers, N. 1990. Scrub and high pine. Pp. 150–193. *In* Ecosystems of Florida. (R.L. Myers, J.J. Ewel, eds.). University of Central Florida Press, Orlando, FL.
- Riechert, S.E. 1976. Web-site selection in the desert spider *Agelenopsis aperta*. *Oikos* 27:311–315.
- Webb, S.D. 1990. Historical biogeography. Pp. 70–100. *In* Ecosystems of Florida (R.L. Myers, J.J. Ewel, eds.). University of Central Florida Press, Orlando, FL.
- World Spider Catalog. 2018. World Spider Catalog. Version 19.0. Natural Museum of Natural History Bern, online at <http://wsc.nmbe.ch/>

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