POPULATION DYNAMICS OF THE RED WIDOW SPIDER (ARANEAE: THERIDIIDAE)

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ABSTRACT

Populations of the red widow spider, *Latrodectus bishopi*, in native Florida scrub at the Archbold Biological Station were monitored annually on ten ~0.5 ha transects in late winter from 1987 to 2000. Of 398 *L. bishopi* detected in the study, all but three had their silken retreats built in palmetto leaves. *L. bishopi* at rest in retreats in saw palmetto (*Serenoa repens*) were higher above the ground (~0.5 m) than spiders in scrub palmetto (*Sabal etonia*) (~0.3 m). From a peak of 31 spiders/ha in 1989, the average *L. bishopi* density declined exponentially to only 0.3 spiders/ha in 1997, after which *L. bishopi* densities began to recover. Burning of scrubby transects in spring or summer appeared to have no affect on subsequent *L. bishopi* populations. There were no significant correlations between *L. bishopi* population density and local temperature or precipitation data. These results suggest that undescribed biotic factors may regulate populations of the red widow spider in a density-dependent fashion.

Key Words: *Latrodectus*, Florida scrub, ecology, populations, dynamics, fire

RESUMEN

En diez transectos de ~0.5 ha, determinamos cada invierno de 1987-2000 las poblaciones de la araña *Latrodectus bishopi* en matorral nativo de Florida en la Estación Biológica Archbold. De las 398 *L. bishopi* que encontramos, todos menos tres habían construido sus retiros sedosus entre las ojas de palmitos. Las *L. bishopi* que reposan en el palmito *Serenoa repens* estan más alto (~0.5 m) que ellos que reposan en el palmito *Sabal etonia* (~0.3 m). El promedio densidad de *L. bishopi* disminuyó exponencialmente desde 31 arañas/ha en 1989 a 0.3 arañas/ha en 1997, despues de que las densidades de *L. bishopi* empezaban a recuperar. Quemando el matorral en la primavera o verano no afectó las poblaciones subsiguientes de *L. bishopi*. No había correlaciones significativas entre la densidad de *L. bishopi* y la temperatura o precipitación local. Los resultos sugieren que hay factores biológicos no describido que regular poblaciones de *L. bishopi* en una manera densidad-dependiente.

The red widow spider, *Latrodectus bishopi* Kaston 1938, is endemic to xeric, upland ecosystems found in Central and Southeastern Florida (Levi & Levi 1990; Edwards 1994). It is restricted to sand pine scrub and scrubby flatwoods in several counties that depend on periodic burning to maintain species diversity (McCrone & Levi 1964; McCrone & Stone 1965; Kaston 1970; Levi & Levi 1990; Abrahamson et al. 1984). Little is known about this rare spider. In large part this stems from the fact that it is difficult to find, even when it is locally abundant. Although *L. bishopi* builds a large tangled web on palmetto shrubs (McCrone & Levi 1964; Edwards 1994; Sierwald & Fenzl 1999), the very fine silk is not highly visible in bright sunlight. Furthermore, its funnel-shaped, silken retreat usually is hidden within a folded palmetto leaf (McCrone & Levi 1964; Sierwald & Fenzl 1999). Field biologists studying vertebrates at the Archbold Biological Station in Highlands County, Florida, have noticed that local populations of the *L. bishopi* seem to erupt every 10-20 years. Early reports suggested mild winters and periods of drought subsequently result in an increased abundance of spiders of the genus *Latrodectus* in many regions of the world (Chamberlain & Ivie 1935).

This study was undertaken in order to gain basic knowledge about the interannual population dynamics of *L. bishopi*. Specifically, I censused web-sites of subadult and adult female *L. bishopi* in ten replicate tracts of native scrub annually for twelve out of fourteen years in a row at the Archbold Biological Station to ascertain long-term changes in population density. I identified the plant species used for a retreat and twice during the study I measured the height of each spider's retreat above the ground as an indication of website preference by *L. bishopi*. In addition, I used a null model to test the short-term affect of fire on the density of *L. bishopi*. Finally, using weather data obtained from Archbold records, I tested whether density of *L. bishopi* is correlated in a simple way with temperature or precipitation.

MATERIALS AND 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 of the study area ranges from approximately 38 to 46 m above mean sea level. The predominant vegetative associations in the study area are scrubby flatwoods, which are dominated by low shrubby oaks (*Quercus inopina*, *Q. chapmanii, Q. geminata*) and palmettos (*Serenoa repens* and *Sabal etonia*). Interspersed among the scrubby flatwoods to varying degrees are two other vegetative associations: sand pine scrub, with widely scattered stands of sand pine (*Pinus clausa*) and an understory of xerophytic shrubs, and flatwoods, with open stands of south Florida slash pine (*P. elliottii* var. *densa*) and an understory and ground cover of mesic grasses, herbs, saw palmetto (*Serenoa repens*), and assorted shrubs (Abrahamson et al. 1984).

Spider Censuses

In 1987 Mary Haskins, Zhaofen Yang, and I discovered that *L. bishopi* webs are easily seen and reliably identified from a distance of many meters at dawn on very foggy mornings because the dew-laden cobweb is highly reflective. Using this knowledge, I devised a drive-by method to census *L. bishopi* in scrub on the side of primitive, sandy roads that pass through the scrub. I established a total of ten permanent, roadside transects in scrub that had been burned in 1984 or 1985. Each transect extended 10 m from the road into the scrub and ranged in length from 375 to 730 m. The average area (±SE) of each transect was 0.55 ± 0.03 ha. At dawn on foggy mornings in late winter (February-early March), I drove slowly (1-3 km/h) in a light truck along the edge of each transect, looking from a height of ~2 m into the scrub for *L. bishopi* webs. Upon sighting a web, I stopped the truck, walked to the web, located the spider in its retreat, and marked the web-site with surveyor tape tied 1-2 m high on nearby vegetation. After repeating each drive-by survey three or four times within a 2 week period, I ceased to find additional webs. Subsequently during the daytime I revisited each *L. bishopi* web-site, carefully opened the retreat, noted whether it was occupied by an adult or an immature female, and recorded the species of plant used by a spider for its retreat. In 1989 and 1999 I also measured the height of *L. bishopi* retreats in the two species of palmettos.

To verify the efficacy of the drive-by method for detecting *L. bishopi* webs, in the second year of the study (1989) I walked through each transect during daytime (0900-1600 h) looking for *L. bishopi* webs several days before I began the drive-by censuses. I visually inspected the leaves of every palmetto within a transect at close range (< 1 m). If I found a *L. bishopi* web, I marked its location cryptically by burying a piece of surveyor tape in the sand near it in such a fashion that the tape was not visible from the nearby road. I spent a total of 30 h searching on foot and 20 h driving slowly looking for webs. After the drive-by survey was completed, I compared the number of *L. bishopi* webs detected by the two methods.

Representative specimens of *L. bishopi* were preserved in the collection of arthropods at Archbold. Statistical analyses were performed using SYSTAT (Wilkinson 1989).

Fire Affects on *L. bishopi* Populations

A record of the date, area, and location of fires on the main property at Archbold is kept as part of the fire management plan (Main & Menges 1997). In addition to burns in 1984 or 1985, eight of my transects were burned once and two transects were burned twice during the course of my study. To test the short-term affects of fire on local *L. bishopi* populations, I developed a null model against which to test the observed data. The null model posited that fire in late spring or summer would have no significant affect on *L. bishopi* spider densities determined several months later in winter. Hence, one would expect an equal proportion of transects (1/3) to show an increase, a decrease, or no change in density in winter after the burn event relative to the winter before the burn. The Fisher exact test was used to test the difference between observed and expected outcomes (Zar 1974).

Weather Affects on *L. bishopi* Populations

I conducted my censuses for twelve years (1987-2000, except for 1988 and 1991) late in winter when many of the native shrubs and trees began to flower or produce new foliage. I obtained weather records starting from the official weather center at Archbold, which has been in operation continuously since 1952. As an indicator of long-term climatic conditions that prevail at Archbold, I calculated the 30-year mean value (data for 1952-1981) and the 95% confidence interval (95% C.I.) for four weather parameters: mean daily temperature in winter (Jan., Feb., & Mar.), minimum winter temperature, total annual precipitation, and mean monthly precipitation in winter. Subsequently I compared the same four parameters for each year starting 1985 with the 30-year means to determine whether there were significant annual deviations during my study.

RESULTS

Comparison of Sampling Methods for *L. bishopi*

As summarized in Table 1, searching on foot during the daytime for *L. bishopi* web-sites in the scrub was very inefficient compared to the drive-by method conducted at dawn on foggy mornings. When I searched on foot in 1989, I found a total of

TABLE 1. COMPARISON OF TWO METHODS FOR FINDING WEB-SITES OF RED WIDOW SPIDERS (*LATRODECTUS BISHOPI*) (N = 168) IN 1989. INITIALLY ALL TEN TRANSECTS WERE SEARCHED ON FOOT DURING DAYTIME AND WEB-SITES WERE CRYPTICALLY MARKED. SUBSEQUENTLY THEY WERE CENSUSED AGAIN AT DAWN AND DEW-LADEN WEB-SITES WERE MARKED.

	Number of web-sites detected			
Transect number	On-foot search only	Drive-by search only	By both search methods	Total
1	4	22	28	54
2	1	2	10	13
3	0	0	0	0
4	2	3	5	10
5	1	7	3	11
6	1	8	4	13
7	0	4	0	4
8	1	13	2	16
9	3	14	4	21
10	4	10	12	26
Sum	17	83	68	168
Percent	10.1	49.4	40.5	100.0

85 L. *bishopi* on the ten transects, 68 of which I subsequently detected in the drive-by survey. On the other hand, I detected a total of 151 webs using the drive-by method, 68 of which I had previously found in my laborious searches on foot of the many palmettos in the transects. Hence, searching on foot was only about 50% effective whereas the drive-by method was about 90% effective for finding *L. bishopi*. The webs I missed using the drive-by method often were located low to the ground and on the side of a palmetto plant facing away from the road. Because the drive-by method seemed to be a reasonably accurate way of censusing *L. bishopi* populations, I adopted it throughout the remainder of the study.

Plants Used by *L. bishopi* for Web-sites

Of 398 *L. bishopi* detected in this study, 395 (99.2%) had their retreats located in leaves of palmettos. Two *L. bishopi* had retreats hidden beneath leaves of staggerbush, *Lyonia fruticosa* (Michx.) Torr. [Ericaceae] and a third spider was resting in a retreat spun under leaves of sand live oak, *Quercus geminata* Small [Fagaceae]; both plants are evergreen shrubs.

L. bishopi used saw palmettos (*Serenoa repens*) as web-sites much more often than scrub palmettos (*Sabal etonia*). As indicated in Table 2, 75-80% of *L. bishopi* webs in 1989 and 1999 were in saw palmettos and 20-25% were in scrub palmettos. Analysis of variance revealed that the

TABLE 2. HEIGHT ABOVE GROUND (M) OF FEMALE RED WIDOW SPIDERS (*LATRODECTUS BISHOPI*) RESTING IN SILKEN RETREATS AS A FUNCTION OF THE PALMETTO SPECIES SELECTED FOR WEB CONSTRUCTION.[A]

Year	Saw palmetto (*Serenoa repens*)	Scrub palmetto (*Sabal etonia*)
1989	0.51 ± 0.02 [a]	0.32 ± 0.03 [b]
1999	0.47 ± 0.03 [a]	0.33 ± 0.04 [b]

[a] Means ± standard errors followed by the same letter are not significantly different by ANOVA followed by Tukey HSD test ($P \geq 0.05$).

height of a *L. bishopi* retreat off the ground was highly dependant on the palmetto species ($F = 21.36$, $P < 0.0001$), but not the year of sampling or the species*year interaction. On average *L. bishopi* retreats in saw palmettos were about 0.5 m above ground, whereas those in scrub palmettos were only 0.3 m above the sandy soil. Because the distance from a *L. bishopi* retreat to the top of a typical palmetto leaf was about 0.3-0.4 m (J. Carrel, unpublished data), this means that the maximal height of palmettos harboring *L. bishopi* generally was below 1.0 m.

Annual Changes in Density of *L. bishopi*

The density of *L. bishopi* declined one hundredfold from 1989 until 1998, but thereafter it began to increase (Fig. 1). The highest mean density (±SE), achieved in 1989, was 30.7 ± 8.1 *L. bishopi*/ha and the lowest mean density, achieved in 1997, was 0.27 ± 0.27 *L. bishopi*/ha. The decade-long decline in mean *L. bishopi* density was highly exponential. If Y = mean *L. bishopi* density

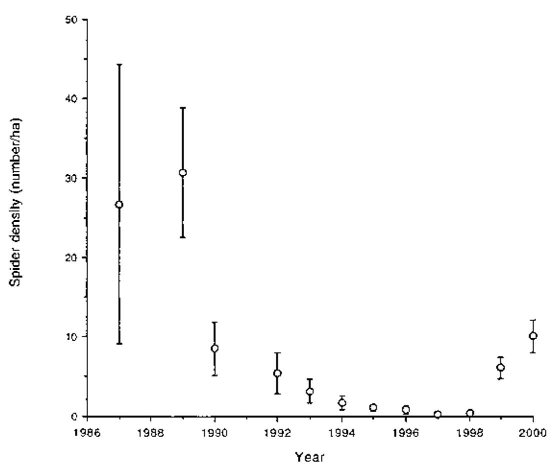

Fig. 1. Annual variation in density of red widow spiders (*Latrodectus bishopi*) at the Archbold Biological Station, Lake Placid, FL. Means ± standard errors are indicated (N = 10 permanent transects).

in year X, and X = 1 for the year 1989 and X = 10 in 1998, then the best fit regression equation is: $Y = 30.827\ (10^{-0.2332X})$ and the correlation coefficient is highly significant ($R = 0.977$, $df = 8$, $P < 0.0001$).

The steady increase in *L. bishopi* densities that occurred from 1998 to 2000 suggests that local spider populations may erupt in the near future. If this were to happen, then in 2003-2005 *L. bishopi* populations would resemble those found in 1987-1989.

Affect of Burning on *L. bishopi* Density

Burning of the scrub in late spring or summer had no affect on subsequent *L. bishopi* spider populations. The observed changes in *L. bishopi* density on any transect were identical to the expected values based on the null model. Of the 12 burn events on transects that happened in the course of this study, four corresponded with increases in *L. bishopi* density, 4 with decreases in *L. bishopi* density, and four with no change in *L. bishopi* density. These results are not very surprising considering the long period of time (~6-10 months) between the occurrence of a fire and my field measurements of spider densities. For example, the palmettos and some other shrubs had fully regenerated many new leaves by the time I conducted my censuses in winter.

Affect of Weather on *L. bishopi* Density

In 1987 and 1989 when *L. bishopi* densities were highest, temperatures were unusually cold (Fig. 2) and precipitation was normal in winter but relatively low during the remainder of the year (Fig. 3). However, in 1990 when *L. bishopi* densities fell greatly compared to the year before, conditions were unusually warm and somewhat dry. In fact, the minimum daily temperature in winter 1990 never dipped below 3.3°C, making this winter the least extreme on record at Archbold.

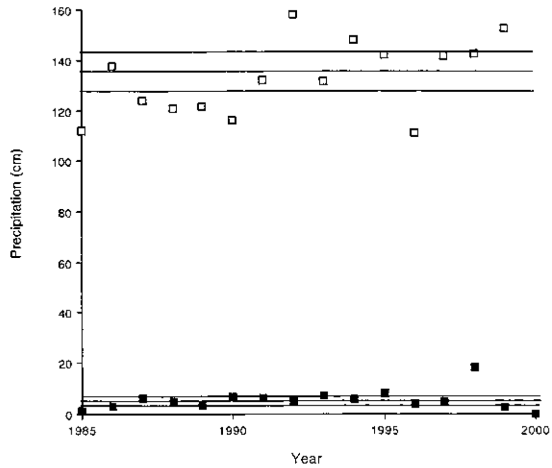

Fig. 3. Total annual precipitation (open squares) and mean monthly precipitation in winter (solid squares) from 1985 to 2000 at the Archbold Biological Station, Lake Placid, FL. Each set of three horizontal lines indicates the 30-year mean ± the 95% confidence interval for both types of data.

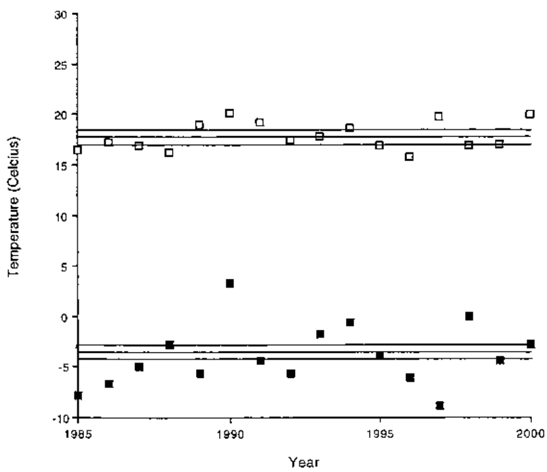

Fig. 2. Mean daily temperature in winter (open squares) and minimum temperature in winter (solid squares) from 1985 to 2000 at the Archbold Biological Station, Lake Placid, FL. Each set of three horizontal lines indicates the 30-year mean ± the 95% confidence interval for both types of data.

Annual *L. bishopi* density was not correlated ($r < 0.45$, $P > 0.05$, $df = 9$ or 10) with any of the temperature or precipitation indices I used (see Methods section). Hence, there was no evidence that weather limits *L. bishopi* populations in a straightforward fashion.

DISCUSSION

Regulation of Spider Populations

Interannual variation in the density of spiders, like those of other animals, can be caused both by abiotic and by biotic factors (Price 1975;Watson & Ollason 1982; Askew & Yalden 1985; Gaston & McArdle 1993; Wise 1993). The lack of a significant correlation between *L. bishopi* density and temperature, precipitation, or fire events during my long-term, highly replicated study suggests that abiotic factors probably did not determine the pattern of change observed in *L. bishopi* populations. On the other hand, the exponential decline in spider densities from 1989 to 1998 implies that a density dependent mechanism might regulate *L. bishopi* populations.

Although there seem to be no long-term studies of population dynamics for any other *Latrodectus* species, there is good evidence that natural enemies commonly limit spider population densities (Wise 1993 and references therein). Candidate species that effectively prey in a density-sensitive fashion on immature and adult *L. bishopi* are the sphecid wasps *Chalybion californicum* and *Sceliphron caementarium* and the Florida scrub-jay *Aphelocoma coerulescens.* These three species are known to eat *L. bishopi* at Archbold (M. Deyrup and G. Woolfenden, unpublished observations) and, more generally, they are known to modify their feeding habits in response to changes in the relative abundance of prey (Coville 1987; Woolfenden & Fitzpatrick 1984). In addition, theridiid spiders of the genus *Argyrodes* living in *L. bishopi* webs may do more than act as kleptoparasites stealing the host's prey; these small spiders may prey on their hosts (Sierwald & Fenzl 1999). Finally, scelionid wasps of the genus *Idris* may contribute significantly to regulation of *L. bishopi* populations since these tiny animals could easily exhibit both functional and numerical responses as their food base changes. *Idris* is the largest genus of insects at Archbold, consisting of many undescribed species about which little is known except that they specialize in feeding on insect and spider eggs (M. Deyrup, unpublished results).

Site Selection by Widow Spiders

Results presented here indicate that *L. bishopi* strongly prefers saw palmetto (*Serenoa repens*) more than all other shrubs for web-sites. The cause of this preference is not clear. Whether chance or necessity determines habitat selection in web-building spiders has been investigated to a limited extent (Lubin et al. 1993; Wise 1993; Foelix 1996). Considering that palmettos comprise the dominant shrub type in burned scrub at Archbold and saw palmetto is much more common than scrub palmetto (*Sabal etonia*) (Abrahamson 1995), a fully probabilistic model for site selection might generate the observed *L. bishopi* web-site data.

Alternatively, a deterministic process of site selection by *L. bishopi* might involve two aspects of palmetto architecture. First, there is a major difference in the patterns of growth between the two palmetto species. The central axes of saw palmetto leaves originate in expanded basal sheaths extending upward from terminal tufts on horizontal stems just above or at the soil surface, whereas scrub palmetto leaves arise on axes extending up from subterranean stems. *L. bishopi* females occasionally use the tubular spaces in leaf bases of saw palmettos for their retreats, which they cannot do with scrub palmettos. Perhaps young *L. bishopi*, as they disperse from their natal web and actively search for protected sites near the soil surface, preferentially select the terminal tufts on saw palmettos and then tend to remain there as they grow and mature.

Second, saw palmettos consistently have more leaves packed densely in narrower crowns than scrub palmettos. Consequently, saw palmetto leaves often overlap and self-shade (Abrahamson 1995). This suggests that the arrangement of saw palmetto leaves may offer *L. bishopi* more protection from enemies and from thermal extremes than scrub palmetto leaves. Lubin et al. (1993) reported comparable evidence for the desert widow spider, *L. revivensis*: selection of larger shrubs in the Negev desert improves spider survival, growth, and reproductive success. But the cost of moving to new web-sites for desert widow spiders is high (40%) mortality. Experiments designed to determine mechanisms and the cost/benefit ratio of web-site selection by *L. bishopi* in Florida scrub are in progress.

Implications for Conservation of Rare Spiders

The *L. bishopi* is restricted to scrub habitats that are remnants of ancient islands in peninsular Florida, now recognized collectively as a major site of biotic endemism (Deyrup & Eisner 1993). But Florida scrub is threatened by loss of habitat resulting from rapid development and by fragmentation that limits gene flow and heightens the probability of extinction in local populations. Recently Skerl (1999) recommended that spiders which are naturally rare because they have highly restricted ranges might be listed nationally as "species of conservation concern," even if they are locally abundant. In addition, Skerl and Gillespie (1999) advocated targeting for conservation action spiders with narrow habitat requirements, limited dispersal abilities, restricted ranges, and immediate threats. *L. bishopi* seems to meet all of their criteria. Hence, I suggest that *L. bishopi* be listed as a species of conservation concern and that its populations be surveyed in peninsular Florida in order to determine the limits of its distribution.

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