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RED WIDOW SPIDERS (ARANEAE: THERIDIIDAE) PREY EXTENSIVELY ON SCARAB BEETLES ENDEMIC IN FLORIDA SCRUB

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ABSTRACT

The red widow spider, *Latrodectus bishopi* Kaston, is a species of conservation concern because it is narrowly endemic to threatened palmetto scrub found only on ancient sand ridges in peninsular Florida. We hypothesized that this spider might feed extensively on insects that also are scrub specialists. To ascertain the prey of red widow spiders, we collected arthropods trapped in webs of adult females (n = 30 per season) located in native oak-palmetto scrub at the Archbold Biological Station after dawn and before dusk for 5 consecutive days in early spring (Mar 1989) and in late spring (May 2003). We identifed a total of 42 species among the 98 specimens collected. Using published regression equations, we converted the size of each specimen to dry mass. We found that 5 species of scarab beetles endemic to Florida scrub accounted for 65% of prey by weight even though their numbers were modest (22% of prey items). In early spring red widow spiders fed predominantly on nocturnally captured coleopterans (78% of prey items), but in late spring when palmetto flowers were blooming near webs day-active hymenopterans were added to the diet. Frequency analysis showed that temporal patterns of prey capture by individual spiders were infrequent (≤ 0.4 prey per day) and statistically random.

Key Words: *Latrodectus*, predation, prey selection, endemism, conservation biology

RESUMEN

Para determinar las presas de la araña viuda roja, *Latrodectus bishopi* Kaston, recolectamos los artrópodos atrapados en las redes de las hembras adultas (n = 30 por estación), ubicadas en los matorral de robles y palma Sabal nativos en la Estación Biológica Archbold después del amanecer y antes del anochecer para 5 días consecutivos días a principios de primavera (marzo de 1989) y en el final de la primavera (mayo de 2003). Identificamos un total de 42 especies, entre las 98 muestras recolectadas. Utilizando las ecuaciones de regresión publicadas, convertimos el tamaño de cada muestra a la masa seca. Se encontró que 5 especies de coleópteros endémicos del matorral Florida representaron el 65% de las presas en peso a pesar de que sus números fueron modestos (22% de las presas). A principios de la primavera las viudas rojas se alimentan predominantemente de coleópteros capturados en la noche (78% de las presas), pero al final de la primavera, cuando las flores de la palma Sabal se florecían cerca de las redes, se han añadido a la dieta los himenópteros activos durante el día. El análisis de frecuencias mostró que los patrones temporales de la captura de la presa de arañas individuales fueron poco frecuentes (≤ 0.4 presas por día) y estadísticamente al azar.

Palabras Clave: *Latrodectus*, depredación, selección de presas, endemismo, biología de la conservación

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The red widow spider, *Latrodectus bishopi* Kaston or RWS, is restricted to xeric, fire-maintained sand pine scrub and scrubby flatwoods found on ancient, sandy ridges in Central and Southeastern Florida (Kaston 1938, 1970; McCrone & Levi 1964; McCrone & Stone 1965; Edwards 1994; Carrel 2001; Levi & Levi 2002). Typically adult *L. bishopi* females build large, tangled capture webs of fine silk extending horizontally for approximately 1 m from palmetto (*Serenoa repens* (Bartram) J. K. Small; Arecales: Arecaceae) leaves to other shrubs that are less than 1.5 m tall. The spiders spend most of their lives hidden in funnel-shaped, silken retreats located beneath the tangle web within a folded palmetto leaf (McCrone & Levi 1964; Sierwald & Fenzl 1999; Carrel 2001). After a sizeable insect enters the tangle web, the resident spider rushes to the point of impact, wraps it quickly in silk, bites the struggling animal to inject paralytic venom, and then trans-

ports the immobilized victim back to the retreat where the prey is eaten and eventually discarded (McCrone & Levi 1964; J. E. Carrel unpublished). Photographs of *L. bishopi* may be found in McCrone & Stone (1965) or Short & Castner (1997).

Despite a widespread and long-standing interest in venomous widow spiders (*Latrodectus* spp.), little more than anecdotal information about predatory habits and ecology in native ecosystems is available for most species (Lawson 1933; Burt 1935; Chamberlin & Ivie 1935; D'Amour et al. 1936; Kaston 1938, 1970; Meacham 1947; Robinson 1947; Levi 1959; McCrone & Levi 1964; McCrone & Stone 1965; Gentry 1974; Krell & Wild 1994; Salomon 2011). An exception to this generalization is the desert widow spider, *L. revivensis* Shulov, which builds its web from the ground up 0.2-0.6 m into low growing shrubs in the Negev Desert (Shulov 1948; Konigswald et al. 1990; Lubin et al. 1991, 1993). The prey of *L. revivensis*, which consists mostly of tenebrionid beetles, is positively correlated with the taxonomic diversity of terrestrial arthropods available in the desert (Shulov 1948; Lubin et al. 1993).

Knowing that *L. bishopi* is endemic to Florida scrub, we hypothesized that this spider might feed extensively on insects that also are scrub specialists, possibly as a result of evolutionary events dating back to the Pliocene and Pleistocene (Deyrup 1989; Deyrup & Eisner 1993, 1996; Menges 1999). Alternatively, *L. bishopi* might be an opportunistic predator having a diet consisting more-or-less of a random assortment of aerial arthropods.

Materials and Methods

Study Area

The Archbold Biological Station (ABS) is located 12 km south of the town of Lake Placid in Highlands County, Florida, near the southern terminus of the Lake Wales Ridge (N 27° 11' W 81° 21'). The predominant vegetative associations in the study area, approximately 350 ha of the Station that is very flat (elevation 38-46 m asl), are scrubby flatwoods, which are dominated by low shrubby oaks (*Quercus inopina* Ashe, *Q. chapmanii* Sargent, *Q. geminata* Small) and palmettos (*Serenoa repens* (Bartram) and *Sabal etonia* Swingle; Arecales: Arecaceae). Interspersed among the scrubby flatwoods to varying degrees are 2 other vegetative associations: sand pine scrub, with widely scattered stands of sand pine (*Pinus clausa* (Chapman); Pinales: Pinaceae) and an understory of xerophytic shrubs, and flatwoods, with open stands of south Florida slash pine (*Pinus elliottii* var. *densa* Little & Dorman) and an understory and ground cover of mesic grasses, herbs, saw palmetto, and assorted shrubs (Abrahamson et al. 1984; Deyrup & Deyrup 2012). See Menges (1999) for more details about ecology and conservation of Florida scrub. All field sites had been burned 2-5 yr before our field studies.

Prey of Red Widow Spiders

We used a drive-by method (Carrel 2001) to search for webs of RWS females for 7-10 days in Mar, May, and Sep over the course of 24 years (1989-2013). Only in 2 of the 72 periods did we detect many RWS webs, reflecting in large part the propensity of RWS populations to "crash" for about a decade after a few years of abundance (declining from 30 to 0.3 spiders/ha; Carrel 2001).

In late Mar 1989 and again in early May 2003, we located 30 webs occupied by adult RWS females within 1-10 m of primitive roads crossing scrubby flatwoods. Initially we removed all prey hanging in each web in late afternoon, then we returned after dawn (0700-0900 h) and before dusk (1700-1900) for 5 days in a row and carefully removed with forceps all arthropods trapped in a web. We noted whether each prey item was located in a spider's retreat or in its tangle web. Specimens were preserved in 70% isopropyl alcohol, returned to the lab, and identified to species. Following the period of daily prey removal, we fed each spider by gently tossing an assortment of beetles and crickets into a web in order to approximate the nutritional state it would have had if left undisturbed.

We measured the body length of each prey item to the nearest 0.1 mm under a dissecting microscope using an ocular micrometer. Appendages such as antennae and ovipositors were excluded. We also measured the width of the thorax or abdomen, whichever was wider. We estimated dry body mass to the nearest 0.1 mg using taxa-specific regression equations (Sample et al. 1993; Sabo et al. 2002). Differences in captured prey were evaluated using the Chi square test with Yates' correction for continuity or the Poisson distribution (Krebs 1989; Gotelli & Ellison 2013).

Results

At the start of our field tests, we found most RWS webs were devoid of prey. In Mar and May we did not detect any arthropods in 90% and 70%, respectively, of webs occupied by adult female spiders. There was no statistically significant difference between prey abundance per spider at the start of the 2 test periods ($\chi^2_c = 5.32$, $df = 3$, $P = 0.15$). Combining the initial data for all 60 spiders, we calculated that a total of 19 insects were hanging in twelve webs and the range was small (≤3 prey per spider). Hence, on average only 1 in 5 RWS females initially had a prey in her web.

As shown in Table 1, the rate of prey capture by RWS females increased by 65% from early to late

TABLE 1. CONTRAST BETWEEN THE TAXONOMIC COMPOSITION OF PREY CAPTURED BY FEMALE RED WIDOW SPIDERS (N = 30) FOR 5 DAYS AND NIGHTS IN EARLY VS. LATE SPRING. THE SEASONAL DIFFERENCE WAS SIGNIFICANT (χ^2_c = 12.64, DF = 2, P = 0.0017). DATA FOR TAXA MARKED WITH AN ASTERISK WERE LUMPED TOGETHER FOR STATISTICAL ANALYSIS.

	Number of individuals captured	
Order	March 1989	May 2003
Coleoptera	29	26
Hymenoptera	3	26
Homoptera*	4	1
Orthoptera*	1	1
Diptera*	0	2
Heteroptera*	0	2
Blattaria*	0	2
Araneae*	0	1
Total	37	61

spring, rising from 0.25 prey/spider/day in Mar to 0.41 prey/spider/day in May. In both sampling periods almost all prey (> 92%) were found in the silken retreats occupied by resident females. In addition, the diversity of arthropods caught by RWS females rose significantly from 4 to 8 orders (Table 1, P = 0.0017). Inspection of the data in Table 1 revealed that the difference was driven by the addition in May of many hymenopterans and some other insects that are known to visit palmetto flowers of the kind near most spiders' webs. Hence, in early spring RWS females specialized on flying coleopterans (78% of prey) but as the season progressed they expanded their prey base to include many other insects.

We found most prey items in RWS webs after dawn in early spring (Table 2), indicating that the spiders were catching insects that were crepuscular or nocturnal, particularly flying beetles. In late spring we detected a significant shift in predation activity toward a slight preponderance of diurnally active insects, especially Hymenoptera. With the advent of flowering by plants, particularly palmettos, and the increased abundance of pollen-feeding bees and wasps in the scrub as spring progressed, the temporal and taxonomic diversity of prey caught by RWS females also increased. Hymenoptera account for 40% of insects species visiting saw palmetto flowers at ABS (Deyrup & Deyrup 2012).

TABLE 2. CONTRAST BETWEEN THE TIME OF DAY WHEN PREY WAS CAPTURED BY FEMALE RED WIDOW SPIDERS (N = 30) FOR 5 DAYS AND NIGHTS IN EARLY AND LATE SPRING. THE TEMPORAL DIFFERENCE WAS SIGNIFICANT (χ^2 = 6.27, DF = 1, P = 0.012).

	Number (%) of prey captured	
Time of day	March 1989	May 2003
Night	26 (70)	27 (44)
Day	11 (30)	34 (56)
Total	37	61

In both sampling periods we found that the observed day-to-day pattern of prey capture matched very closely the predicted distribution from the Poisson model (Mar: $\overline{\chi}$ = 1.03 days with prey, χ^2 = 3.31, df = 5, P = 0.65; May: $\overline{\chi}$ = 1.70 days with prey, χ^2 = 1.63, df = 5, P = 0.90). Thus, the temporal pattern of prey capture by RWS females was statistically random and relatively uncommon. This suggests prey capture by RWS females was fairly homogeneous in each sample period, and little affected by site-to-site differences or by the presence of previously captured insects in webs.

We identified and measured a total of 43 species taken from webs of RWS females (Table 3). Using data in Table 3, we noted that scarab beetles were a major component of the diet both in early and late spring (59% and 36%, respectively). Furthermore, 5 species of scarab beetles known to be endemic to Florida scrub accounted for the majority of the prey dry mass in our samples (80% and 55% in Mar and May, respectively). These results suggest that RWS females may have evolved to specialize in feeding on native coleopterans.

DISCUSSION

We found that 5 species of coleopterans endemic to Florida scrub were the main component in the diet of RWS females (65% of prey by weight) even though their numbers were modest (22% of prey items). Furthermore, all of these prey items were acquired by spiders between dusk and dawn, suggesting that flight activity of most beetles was nocturnal. This is consistent with previous research using aerial intercept traps that showed most coleopterans fly in the dark at 1-1.5 m elevation just above the shrub matrix where the *L. bishopi* locate their tangled capture webs (Carrel 2001, 2002; J. E. Carrel unpublished).

A significant result of our study is the paucity of ants in the RWS webs. We obtained 1 alate queen fire ant (*Solenopsis invicta* Buren), which represented 1.0% and 0.02% of total prey by count and mass, respectively. In contrast, *Latrodectus pallidus* Cambridge in Israel, *L. hesperus* Chamberlin & Ivie in California, and *L. mactans* (F.) in east Texas are mainly predators of ants (Shulov & Weissman 1959; MacKay 1982; Nyffeler et al. 1988). Even at 48° N latitude in cool, wet coastal British Columbia, Canada, ants comprise 14% of prey items in webs of *L. hesperus* (Salomon 2011). These three widow spiders, like many other theridiids, build their tangle webs close to the ground

TABLE 3. TAXONOMIC IDENTITY, NUMBER OF INDIVIDUALS, AND ESTIMATED DRY MASS OF PREY CAPTURED BY FEMALE RED WIDOW SPIDERS (N = 30) FOR 5 DAYS AND NIGHTS IN EARLY VS. LATE SPRING.

			March		May	
Order	Family	Species	Number	Dry mass (mg)	Number	Dry mass (mg)
Araneae	Lycosidae	*Gladicosa* sp.	—	—	1	11.2
Blattaria	Blatellidae	*Parcoblatta fulvescens* (Saussure & Zehnter)	—	—	2	76.2
Coleoptera	Cantharidae	*Polemius laticornis* Say	—	—	1	2.5
	Chrysomelidae	*Caryobruchus gleditsiae* (Linnaeus) †	1	15.5	—	—
		Hemisphaerota cyanea (Say)	2	18.2	—	—
		Neochlamisus insularis (Schaeffer)	1	5.0	—	—
		Unknown	1	3.8	—	—
	Coccinellidae	*Exochomus childreni* (Mulsant)	1	2.8	—	—
	Lycidae	*Plateros flavoscutellatus* Blatchley †	—	—	1	3.2
	Scarabaeidae	*Boreocanthon probus* (Germar)	—	—	1	12.6
		Diplotaxis bidentata LeConte †	8	176.8	2	44.2
		Euphoria limbalis Fall †	—	—	1	60.8
		Hypotrichia spissipes LeConte *	—	—	5	301.0
		Onthophagus hecate blatchleyi Brown	—	—	1	17.1
		Phyllophaga elizoria Saylor *	14	1241.8	—	—
		Phyllophaga elongata (Linell) *	—	—	9	798.3
		Serica frosti Dawson *	—	—	1	19.1
		Trigonopeltastes floridana (Casey) * †	—	—	2	36.0
	Tenebrionidae	*Hymenorus* sp. †	—	—	2	13.6
		Statira dolera Parsons	1	11.9	—	—
Diptera	Otitidae	*Euxesta* sp.	—	—	1	1.6
	Sarcophagidae	Unknown	—	—	1	2.1
Heteroptera	Coreidae	*Acanthocephala confraterna* (Uhler)	—	—	2	195.6
Homoptera	Cercopidae	*Prosapia bicincta* (Say)	—	—	1	12.2
	Cicadellidae	*Jikradia melanota* (Spangberg)	1	1.2	—	—
		Unknown	2	28.8	—	—
	Flattidae	*Flatoidinus punctatus* (Walker)	1	2.9	—	—
Hymenoptera	Apidae	*Apis mellifera* Linnaeus †	—	—	9	252.9
	Evaniidae	*Hyptia reticulata* (Say)	—	—	1	1.0
	Formicidae	*Solenopsis invicta* Buren †	—	—	1	6.5

*Species know to be endemic to Florida scrub.
†Species know to visit palmetto flowers (Deyrup & Deyrup 2012).

TABLE 3. (CONTINUED) TAXONOMIC IDENTITY, NUMBER OF INDIVIDUALS, AND ESTIMATED DRY MASS OF PREY CAPTURED BY FEMALE RED WIDOW SPIDERS (N = 30) FOR 5 DAYS AND NIGHTS IN EARLY VS. LATE SPRING.

			March		May	
Order	Family	Species	Number	Dry mass (mg)	Number	Dry mass (mg)
	Halictidae	*Augochloropsis metallica* (Fabricius) †	—	—	1	10.7
	Pompilidae	*Psorthaspis mariae* (Cresson)	1	13.3	—	—
	Sphecidae	*Hoplisoides* sp.	—	—	1	8.8
	Tiphiidae	*Myzinum maculatum* (Fabricius) †	—	—	8	60.0
		Paratiphia texana Cameron †	—	—	2	5.8
		Tiphia sp.	1	2.9	—	—
	Vespidae	*Pachodynerus erynnis* (Lepeletier) †	—	—	1	48.1
		Parancistrocerus histrio (Lepeletier) †	—	—	1	22.0
		Polistes bellicosus Cresson †	—	—	1	83.2
	Unknown	Unknown	1	2.9	—	—
Orthoptera	Gryllidae	*Orocharis luteolira* Walker	1	27.4	—	—
	Tettigoniidae	Unknown	—	—	1	9.0
		Total	37	1555.2	61	2115.3

*Species know to be endemic to Florida scrub.
†Species know to visit palmetto flowers (Deyrup & Deyrup 2012).

primarily to capture beetles and ants that crawl on the ground (Nyffeler et al. 1988). *Latrodectus bishopi* is atypical in that its web is completely aboreal, starting at 0.2-0.4 m above ground level (Carrel 2001). Another species of *Latrodectus*, *L. variolus* Walckenaer, makes arboreal webs in north Florida (McCrone & Levi 1964). This behavior, combined with morphological similarities between *L. variolus* and *L. bishopi*, led McCrone & Levi (1964) to suggest that *L. bishopi* is derived from a population in the *L. variolus* lineage isolated on sand ridges of peninsular Florida during the Pleistocene.

We clearly recognize that our study was opportunistic, lacking in robust experimental design. The 14-year gap between the early and late spring samples means that seasonality is confounded with year-to-year effects. Abundances of available prey species could have changed dramatically during the long interval. In addition, we did not manipulate the status of palmetto flowers (present or absent) near RWS webs in the May 2003 samples, which we would need to do to demonstrate unambiguously that most hymenopterans caught by RWS females were actually attracted to inflorescences. Lastly, to ascertain whether RWS females actually specialize in feeding on scrub endemic scarabs, we would need to perform replicated trapping of aerial insects simultaneously with sampling RWS prey in the palmetto scrub and then contrast the taxonomic diversity of the two kinds of samples. But because all methods of sampling arthropods moving through the air have major drawbacks (Carrel 2002), differences in the species composition between the two samples would have to interpreted with caution.

To our knowledge the RWS is only the second known predator of adult Florida tortoise beetles, *Hemisphaerota cyanea* (Say), that feed exclusively on palmettos in Florida scrub. Eisner et al. (2005) reported that the assasin bug, *Arilus cristatus* (L.), overcomes the beetle's chemical and mechanical defenses by piercing the body with its sharp rostrum. Besides the 2 prey records in our study, we have recorded 5 additional instances of *H. cyanea* being eaten by RWS females in native scrub (J. E. Carrel unpublished). These field observations were validated in laboratory trials in which we documented more than a dozen instances of *L. bishopi* attacking Florida tortoise beetles placed in their tangle webs and transporting them back to the retreat where they were eaten (T. Eisner & J. E. Carrel unpublished).

Latrodectus bishopi is an ecologically and geographically restricted species that is considered a species of conservation concern (Edwards 1994; Carrel 2001). Although this species is presumably venomous to humans, there are no records of attacks. Our field observations strongly suggest that it would be almost impossible to be bitten by *L. bishopi* without dragging it from its retreat and applying the spider to a sensitive area of skin. Like many other types of toxins, however, the venoms of *Latrodectus* species may have applied value, both in understanding the operation of neuroactive compounds and in the search for new drugs and insecticides (McCormick & Meinwald 1993). One research paper notes a ". . . wave of arachnophilia which has manifested itself in the chemical and pharmacological literature. . . ." (McCormick & Meinwald 1993). While the preservation of species diversity is an end in itself, species diversity also represents a vast library of undiscovered bioactive compounds (Eisner 1992, 1994).

This study deepens our understanding of why *L. bishopi* is restricted to Florida scrub habitat. This species depends on seasonal presence of prey, especially scrub scarabs. The flight patterns of these are dictated by the structure of scrub vegetation, making the beetles susceptible to trapping by *L. bishopi*. The major threat to this species is probably the disappearance of Florida scrub habitat. On the Lake Wales Ridge over 85% of original Florida scrub habitat has been eradicated (Weekley et al. 2008). *Latrodectus bishopi* and many other scrub animals and plants not only need protected habitat, but the habitat must also be managed with fire to mimic natural burns that kept vegetation structure relatively low and even (Carrel 2001).

Superimposed on the threat of dwindling suitable habitat is the pattern of strong population fluctuations, whose causes are unknown, possibly density-dependent predation (Carrel 2001). In theory, these fluctuations might eliminate *L. bishopi* from small "islands" of scrub habitat. The dispersal ability of *L. bishopi* is unknown, but its absence from scrub habitat in several regions of Florida suggests that dispersal is limited. Recently, a new threat to *L. bishopi* may have appeared in the form of the parasitoid *Philolema latrodecti* (Fullaway), a specialized Old World chalcidoid (Eurytomidae) that attacks egg sacs of *Latrodectus* species (Bibb & Buss 2012). This species is now common on the ABS in egg sacs of *L. geometricus* (Koch), itself an introduced species. If this parasitoid, whose population is maintained by *L. geometricus* found around buildings, is able to disperse efficiently into scrub habitat it might depress or eliminate populations of *L. bishopi*.

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