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Journal of Natural History

Publication details, including instructions for authors and subscription information:

<http://www.informaworld.com/smpp/title-content=t713192031>

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Sarah C. Crews^a; Eduardo Wienskoski^b; Rosemary G. Gillespie^a

^a ESPM-Division of Organisms and Environment, University of California, Berkeley, Berkeley, CA, USA ^b Laboratório de Aracnologia, Museu Nacional, Rio de Janeiro, RJ, Brazil

Online Publication Date: 01 January 2008

To cite this Article Crews, Sarah C., Wienskoski, Eduardo and Gillespie, Rosemary G.(2008)'Life history of the spider *Selenops occultus* Mello-Leitão (Araneae, Selenopidae) from Brazil with notes on the natural history of the genus',*Journal of Natural History*,42:43,2747 — 2761

To link to this Article: DOI: 10.1080/00222930802354183

URL: <http://dx.doi.org/10.1080/00222930802354183>

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Life history of the spider *Selenops occultus* Mello-Leitão (Araneae, Selenopidae) from Brazil with notes on the natural history of the genus

Sarah C. Crews^{a*}, Eduardo Wienskoski^b and Rosemary G. Gillespie^a

^aESPM-Division of Organisms and Environment, University of California, Berkeley, Berkeley, CA, USA; ^bLaboratório de Aracnologia, Museu Nacional, Rio de Janeiro, RJ, Brazil

(Received 25 March 2008; final version received 6 June 2008)

Selenopids are extremely fast-moving, dorsoventrally flattened spiders and are among the most secretive of animals. However, they can be locally abundant, providing an opportunity to examine their life and natural histories. Here we report life history data from *Selenops occultus* which were studied and collected monthly for over a year at an experimental farm of São Paulo State University in Botucatu, Brazil. We compare these data with what we have found in other *Selenops* species in the Caribbean region. Overall, *S. occultus* showed considerable seasonality. Males were most common in January and March, whereas females were more common in June and November. Significant differences between the numbers of males collected during the wet and dry seasons indicate that mating may be limited to the wet season. The Caribbean species share similar natural histories to *S. occultus*, such as little conflict in small areas and overlapping generations throughout the year.

Keywords: São Paulo; Caribbean; islands; seasonality

Introduction

The spider family Selenopidae, first described by Simon (1897) comprises fewer than 10 genera and occurs worldwide, primarily in the tropics and subtropics. The current study focuses on the most species-rich genus, *Selenops*, in which 118 species have been described to date. Representatives are large in size (the smallest ones are around 5mm as adults, and the largest up to 20mm), but are among the most secretive of spiders (Muma 1953; Crews 2005) due to their rapidity of movement (up to 63 body lengths/second in *S. lindborgi*), their ability to hide in inaccessible places, and their nocturnal habits. These attributes, coupled with the lack of funds to study and describe the natural history of organisms (Greene 2005), mean that the natural history of the genus is virtually unknown. As a first step towards rectifying the dearth of ecological knowledge of the group, the current study provides (1) a detailed examination of the life history of a relatively widespread representative of the genus, *Selenops occultus* Mello-Leitão, 1918 from Brazil, Paraguay and Argentina (Corronca 1998); and (2) an overview of the available information on ecological affinities and behaviours of multiple species in the Caribbean.

*Corresponding author. Email: screws@berkeley.edu

Methods

Collections

Brazil

Collections of *S. occultus* were made at a single site, a farm for agronomic research and forest engineering at the Universidade Estadual Paulista in Botucatu in the state of São Paulo, Brazil (avg. elevation=800m; 22°50'40.74" S 48°25'33.10" W), over a 2-year period using standardized methods. Spiders were observed and collected during the period from early June 2002 to early October 2003 with collections made every 23 days on average, producing 22 individual collections. The average temperature at this site is 20°C. The rainy season at Botucatu lasts from October to March, with the dry season continuing from April to September. Previously part of an Australian eucalyptus (primarily *Eucalyptus grandis*) plantation, the patch of vegetation where the collections were made is now a secondary growth savannah ciliary forest, a broad-leaved wet forest with periodic flooding (Leitão Filho 1982). All collections were made in the first hours of the night for a 70-minute interval along a sinuous transect of approximately 900m in which all individuals sighted were collected. Due to the tree bark acting as a natural shelter for the spiders, it was not removed, and only spiders that had emerged from under the bark were collected. However, as the spiders are nocturnal, and even females will leave their egg sacs to 'sit and wait' on the other side of the bark, the spiders collected during these 70-minute intervals were likely representative of actual spiders present. A different transect was followed during each collection period to prevent over-exploitation of a previously collected area.

The specimens were categorized as: adult males, adult females, penultimate males, penultimate females, juveniles 4–6mm in size and juveniles under 4mm. Abundance data were then plotted along with the maximum and minimum temperatures and rainfall for the area throughout the study period. A *t*-test was performed using JPM IN (v. 4.0.4; SAS Institute, Duxbury Press) for members of a group collected in the dry season and members of a group collected in the wet season. All *S. occultus* specimens are deposited in Museu Nacional, Rio de Janeiro.

Caribbean

In the Caribbean islands, collections and observations were made at multiple sites over a 4-year period from the beginning of October 2004 to the end of November 2004; July 2005; the beginning of May 2006 to mid-June 2006; July 2006; October 2006 and the beginning of February 2007 to mid-March 2007. The general climate in the Caribbean is subtropical to tropical, with more precipitation in the fall and winter months. Temperature and precipitation vary with elevation; low-lying islands or parts of islands tend to be much dryer and warmer, whereas at high elevations temperature is lower and precipitation is greater. Spiders (14 species) were not collected in a systematic manner, though typical collecting sites were in lower elevations (unless otherwise noted), both during the day and at night. Observations were made of the behaviour and ecology during each collecting period for the following species: *S. micropalpus* Muma, 1953, *S. submaculosus* Bryant, 1940, *S. aissus* Walckenaer, 1837, *S. curazao* Alayón, 2001, *S. lindborgi* Petrunkevitch, 1926, *S. insularis* Keyserling, 1881, *S. candidus* Muma, 1953, *S. bani* Alayón, 1992, *S. pensilis* Muma, 1953, *S. marcanoi* Alayón, 1992, *S. petrunkevitchi* Alayón, 2003, *S.*

phaselus Muma, 1953, *S. simius* Muma, 1953, and *S. cf. geraldinae*. The species names, years and authors were confirmed using the World Spider Catalog (Platnick 2008). All Caribbean specimens will be deposited in the Essig Museum of Entomology at the University of California, Berkeley, and the California Academy of Sciences, San Francisco.

Results

Brazil

A total of 917 *S. occultus* were collected during this study and their abundances are summarized in Figure 1. Adult male spiders were the rarest, and were found consistently only from January to March, with a single male in June of 2002 and two males in May of 2003. Penultimate males were collected consistently from October to February, indicating a 2–3 month time period to reach maturity from the penultimate stage, which is similar to what has been observed in the lab. Adult female spiders were taken throughout the year and were most abundant in June and November. Penultimate females were quite common throughout the year, particularly in August of 2003. Immatures in which sex-determination was not possible were divided by size into two groups (4–6 mm and less than 4 mm). The latter were the most common overall and were most numerous in January. Up to eight *S. occultus* were collected on a single tree simultaneously. No potential

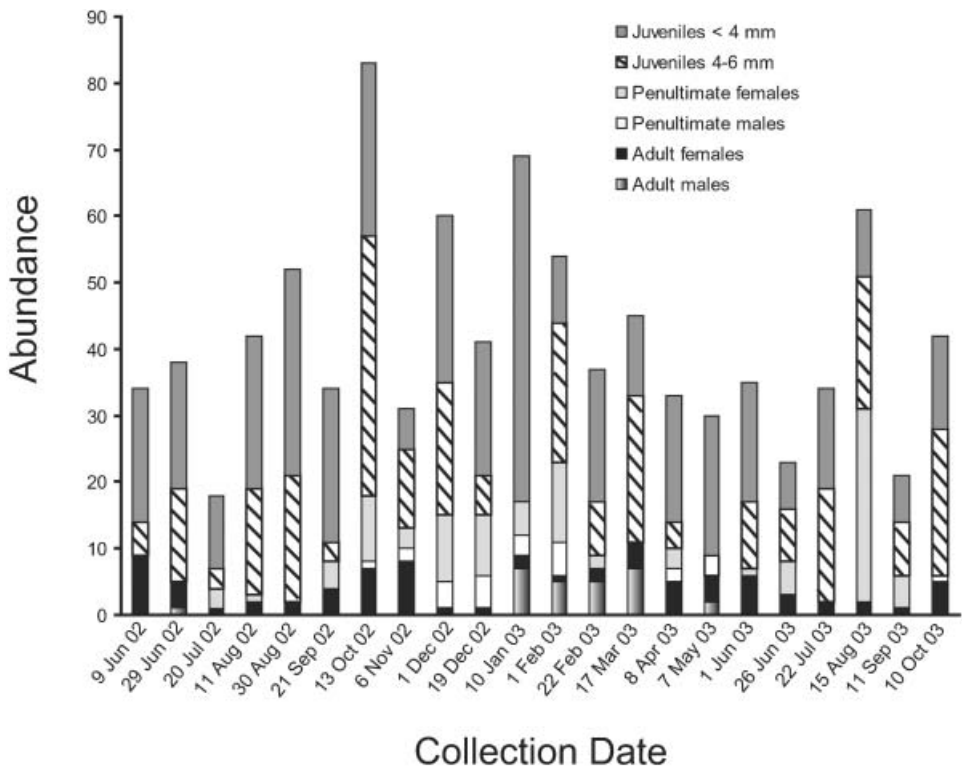


Figure 1. Abundance data for each of the six groups of *S. occultus* for each collection date.

predators were seen and prey items were observed to be cockroaches and small moths.

Within each month, differences between the average minimum and average maximum temperatures were large, but temperature differences between months were not large (Figure 2). The wettest time of the study occurred during October of 2002, peaking in January and April of 2003. There was no rainfall at all in June of 2002 and, incidentally, the smallest number of spiders was found the following month, perhaps indicating high mortality due to desiccation or a limited food supply. However, in October of 2002 the largest number of spiders was found following this dry period, whereas in the next year, which lacked such a dry period, only half of this number was found. A *t*-test indicated significant differences between the number of adult males collected in the dry season versus those collected in the wet season ($p < 0.03$), as well as between the number of penultimate males collected in the dry season versus the number collected in the wet season ($p < 0.005$) (Figure 3). There were no significant differences detected in the number of females, penultimate females, or immature specimens.

Caribbean

The numbers, sexes, localities and collection dates for each species are listed in Table 1. The natural history data we observed, including time of day, habitat, microhabitat, plant species, associated fauna, feeding, egg sac guarding and any additional observations are given in Table 2. In general, it appears that Caribbean

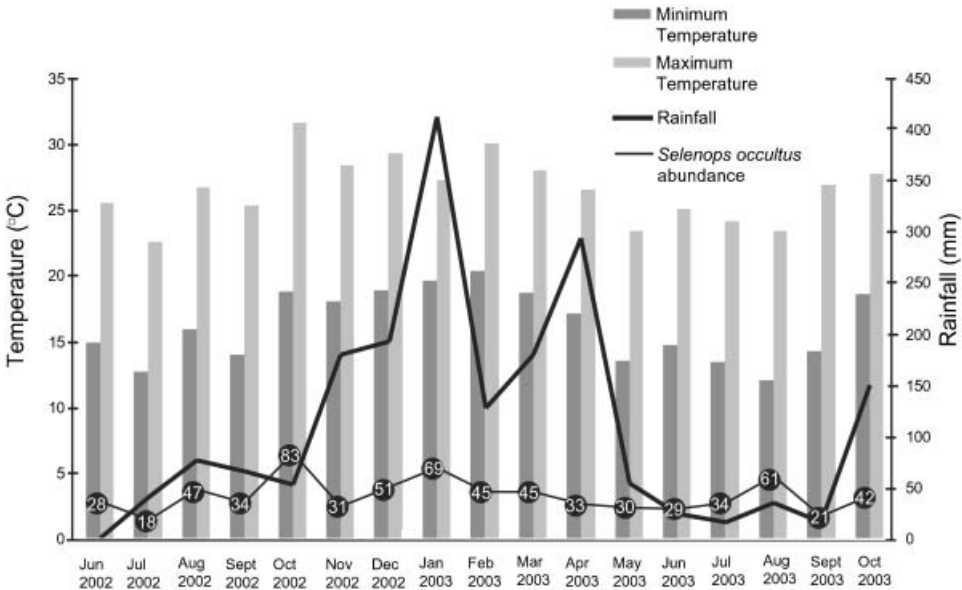


Figure 2. Abundance data for *S. occultus* plotted together with the average monthly precipitation and minimum and maximum temperatures for each month during which the study took place. The numbers in the black circles are the total number of *S. occultus* collected during each month.

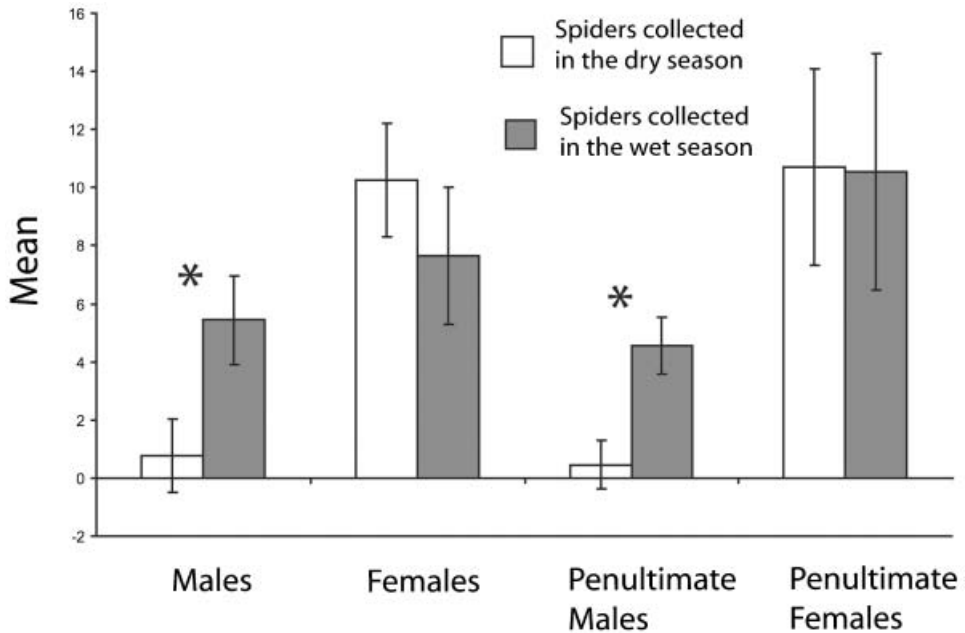


Figure 3. Chart depicting mean numbers of males, females, penultimate males and penultimate females collected during the dry season and the wet season. The data from the immature specimens were omitted to increase the clarity of the graph (the much higher number of immature specimens would greatly increase the scale). The error bars depict the standard error, and the asterisks indicate statistically significant differences between the number of specimens of a group collected during the dry season and the number collected during the wet season.

Selenops are found in a variety of habitats and microhabitats, on several types of plants and with many different types of other organisms. The majority of species appear to guard their egg sacs and to be habitat generalists, though two species are only found at higher elevations in cloud forests.

Discussion

The data presented here are the first of their kind for *Selenops* spiders. Comparing the data from Brazil and the Caribbean, the observation of up to eight *S. occultus* being found on a single tree is similar to that of some of the Caribbean species. For instance, 11 *S. insularis* were collected on a single mahogany tree in Humacao, Barrio Collores, Puerto Rico. These included four different sizes (instars) as well as adults. Indeed, it is not uncommon to find multiple spiders on single trees at night in the Caribbean islands. In some areas of Puerto Rico and the Dominican Republic, two different species (*S. lindborgi* and *S. insularis*) have been taken from the same tree. Also in the Dominican Republic, three different species (*Selenops insularis*, *S. bani*, *S. pensilis*) were found under the same rocks lining a path in a single locality (Lago Enriquillo). The spiders may be able to live without conflict in small areas and appear to remain in the same place for extended periods. In the majority of localities where we have collected *Selenops*, immatures and adults are almost always found at

Table 1. Species collected, the island where they were collected, the sexes of the specimens collected, the quantities of each sex and the dates they were collected.

<i>Selenops micropalpus</i>	Dominica			Martinique			St. Lucia			St. Vincent		
Sex	M	F	I	M	F	I	M	F	I	M	F	I
Quantity	0	2	13	4	9	7	1,1pM	6	15	1	1	7
Date	1–2/Nov/2004			8–10/Mar/2007			12–13/Mar/2007			24–30/Oct/2004		
<i>Selenops submaculosus</i>	Andros Island, Bahamas			Pigeon Cay, Bahamas			Great Exuma, Bahamas					
Sex	M	F	I	M	F	I	M	F	I			
Quantity	2,4pM	13	14	0	1	0	0	1	0			
Date	12–13/May/2006			13/May/2006			18/May/2006					
<i>Selenops aissus</i>	Abaco Island, Bahamas			Great Exuma, Bahamas			Stocking Island, Bahamas			San Salvador, Bahamas		
Sex	M	F	I	M	F	I	M	F	I	M	F	I
Quantity	0	1	1	0	2	5	0	2	5	0	4	7
Date	14/May/2006			18/May/2006			18/May/2006			19/May/2006		
<i>Selenops curacao</i>	Bonaire			Curaçao								
Sex	M	F	I	M	F	I						
Quantity	2pM	6	8	1	1	6						
Date	11–12/Oct/2004			8/Oct/2004								
<i>Selenops lindborgi</i>	Great Inagua, Bahamas			Guana Island, BVI			Tortola, BVI			Virgin Gorda, BVI		
Sex	M	F	I	M	F	I	M	F	I	M	F	I
Quantity	1	0	2	0	2	5	1	0	0	1pM	0	6
Date	16/May/2006			18/Oct/2006			20/Oct/2004			19/Oct/2004		
	Hispaniola			Nevis			St. Kitts			Puerto Rico		
Sex	M	F	I	M	F	I	M	F	I	M	F	I
Quantity	1	4	11	0	2	5	1pM	3	6	7	11	19
Date	29–30/Oct/2004; Jul/2007			23/Feb/2007			24/Feb/2007			6–15/Jun/2006		

Table 1. (Continued.)

	Isla Mona			Culebra			Vieques			St. Thomas, USVI		
Sex	M	F	I	M	F	I	M	F	I	M	F	I
Quantity	0	1	2	1	2	7	1	1	7	1	1	16
Date	Jun/2006; Jan/2007			12/Jun/2006			19/Jun/2006			22,24/Oct/2004; 20/Oct/2004		
	St. John, USVI			St. Croix, USVI								
Sex	M	F	I	M	F	I						
Quantity	2,2pM	1pF	2	0	3	9						
Date	16/Nov/2004			19/Nov/2004;14/Jun/2006								
<i>Selenops insularis</i>	Hispaniola			Puerto Rico			Vieques					
Sex	M	F	I	M	F	I	M	F	I			
Quantity	6,3pM	13	73	5	13	19	1	3	7			
Date	24–30/Oct/2004; Jul/2006; Jul–Aug/2006; 7–23/Oct/2006			6–15/Jun/2006			19/Jun/2006					
<i>Selenops candidus</i>	Jamaica											
Sex	M	F	I									
Quantity	3,1pM	1	10									
Date	27/May–5/Jun/2007											
<i>Selenops bani</i>	Hispaniola											
Sex	M	F	I									
Quantity	2	1	0									
Date	26/Nov/2004											
<i>Selenops pensilis</i>	Hispaniola											
Sex	M	F	I									
Quantity	0	3	2									
Date	26/Nov/2004; Jun/2006											

Table 1. (Continued.)

<i>Selenops marcanoi</i>	Hispaniola											
Sex	M	F	I									
Quantity	4	1	1									
Date	25/Nov/2004											
<i>Selenops petrunkevitchi</i>	Jamaica											
Sex	M	F	I									
Quantity	1	3	8									
Date	1/Jan/2006											
<i>Selenops phaseus</i>	Hispaniola											
Sex	M	F	I									
Quantity	6	2	5									
Date	24/Nov/2004; 20–21/Oct/2006											
<i>Selenops simius</i>	Cayman Brac			Grand Cayman			Little Cayman					
Sex	M	F	I	M	F	I	M	F	I			
Quantity	2	1	3	0	0	4	0	1	0			
Date	3/Oct/2004			30/Sep/2004; 2/Oct/2004			3/Oct/2004					
<i>Selenops cf. geraldinae</i>	Trinidad			Gaspar Grande, Trinidad			Huevos Island, Trinidad			Chacachacare, Trinidad		
Sex	M	F	I	M	F	I	M	F	I	M	F	I
Quantity	0	0	6	4	3	4	1	0	0	0	0	1
Date	11/Jul/2005			12/Jul/2005			13/Jul/2005			13/Jul/2005		
	Monos Island, Trinidad											
Sex	M	F	I									
Quantity	1	0	3									
Date	13/Jul/2005											

Note: M, male; F, female; I, immature; pM, penultimate male; pF, penultimate female; BVI, British Virgin Islands.

the same time (typically four to five different sizes) suggesting overlapping generations at all months of the year. This impression is supported by the data from *S. occultus*. Interestingly, the results of the *t*-test (Figure 3) indicate that penultimate males and adult males are only abundant during the wet season, while similar numbers of penultimate females, females and immatures are found during both the wet and dry seasons. This implies that mating may be limited to the wet season as this is the only time adult males are plentiful.

An exciting outcome from our exploratory field studies is that new species are often encountered (Mondragón 2007; Alayón 2005; Corronca 1998, 2003). We have found over 10 undescribed species during our studies. The natural history of these will be addressed in another publication along with their descriptions.

It is unknown how long the different species live in nature, however, in the lab, we have reared a specimen from Arizona for over 2 years (it was likely a second or third instar when collected and has molted four times; currently it is still at least one to two molts away from adulthood). We have also had adult males from the Caribbean remain alive as adults for over 4 months, and mated adult males from Namibia, Africa remain alive for over a year (S. Crews, unpublished data).

As described above, females of most Caribbean species appear to guard their egg sacs, with the exception of *S. lindborgi*. This species produces several (up to five) egg sacs at a time and leaves them on any surface in a haphazard fashion. In contrast, other species construct a large, flat egg sac, hiding it under bark or other objects, and sitting on top of it. *Selenops insularis*, *S. aissus* and an undescribed species from Montserrat, Guadeloupe and Antigua build a cocoon over the egg sac and sit inside the cocoon on top of the egg sac. After about a month the eggs hatch and the spiderlings remain inside the egg sac for 2–3 weeks. Eventually they emerge, but – at least in a vial – can remain in close proximity to each other and the mother for several more days without conflict. The spiderlings were still able to emerge from the egg sac after the mother had died. In the case of the aforementioned Namibian species, an egg sac was produced in March, the spiders hatched in May and remained in the egg sac until October (S. Crews, unpublished data). The female is still alive and has made two more egg sacs. Data for the egg sacs of *S. occultus* were not available as the spiders likely make their egg sacs under the bark of the trees, and the bark was not removed in this study.

The findings of this study indicate that the spiders appear to be generalists in terms of their microhabitats. For instance, certain eucalyptus species provide an ideal place in both non-native (*S. occultus* in Botucatu and *S. petrunkevitchi* in Jamaica) and native (*S. australiensis* in Australia; Ron Atkinson, personal communication) habitats. The spiders apparently live under the bark of any tree, or in any small space they can fit (beneath rocks, debris on the ground, behind paintings and posters, etc.), both indoors and out.

Although no predators were seen in the forest of Botucatu, it is likely that predators of the spiders exist. However, given that the spiders hide under bark during the day, it seems that only active searching by birds or lizards would uncover them. In the Caribbean, the spiders have been observed to fall prey to the abundant *Anolis* lizards, but this is only after they have been disturbed by the collector from their safe-haven under the bark. On occasion, the spiders have been found out in the open during the day (in Trinidad on a tree, in México on a fence post), but it was presumed that they had previously been disturbed. The only other animal seen (on a

Table 2. Natural history data observed for the Caribbean species.

Species	Time of day observed	Habitat	Micro-habitat	Plant species on which <i>Selenops</i> was found	Associated fauna	Feeding	Egg sac guarding	Additional observations
<i>S. micropalpus</i>	Day	Dry forest, coastal forest, agricultural setting	Under bark, beneath leaves	<i>Bursera</i> , <i>Casuarina</i> (Australian pine); <i>Coccoloba</i> (sea grape); <i>Heliconia</i> , <i>Hematoxylum campechianum</i> (campeche); <i>Mastichodendron foetidissimum</i> (mastic); <i>Pimenta</i> (bay); <i>Swietenia mahogoni</i> (mahogany)	Geophilomorph centipedes; Rhinocricid millipedes; <i>Anolis</i> lizards	–	Yes	–
<i>S. submaculosus</i>	Night and day	Cave entrance, beach, coppice	Under bark, on ceiling of a cave guarding egg sac	<i>Bursera</i> , <i>Casuarina</i> (Australian pine); <i>Coccoloba</i> (sea grape); <i>Metopium toxiferum</i> (poisonwood)	Elaterid beetle; Scytodid spider; <i>Osteopilus septentrionalis</i> (Cuban tree frog)	–	Yes	–

Table 2. (Continued.)

Species	Time of day observed	Habitat	Micro-habitat	Plant species on which <i>Selenops</i> was found	Associated fauna	Feeding	Egg sac guarding	Additional observations
<i>S. aissus</i>	Day	Fern-pine forest, dry forest, beach, Palmetto-sea-grape forest	Under rocks, under bark, under coconuts	<i>Bursera</i> , <i>Casuarina</i> (Australian pine); <i>Coccoloba</i> (sea grape); <i>Metopium toxiferum</i> (poisonwood)	<i>Anolis</i> lizards; <i>Ameiva</i> lizards; <i>Sphaerodactylus</i> geckos; spiders; Cerambycid beetle	–	Yes	–
<i>S. curazao</i>	Day	Urban, dry limestone forest, thornscrub	In houses, under debris on ground, under bark	<i>Acacia</i> , Cactaceae	–	–	Yes	11 Days after an egg sac was produced, 45 babies emerged and remained for 1 week before emerging from the sac

Table 2. (Continued.)

Species	Time of day observed	Habitat	Micro-habitat	Plant species on which <i>Selenops</i> was found	Associated fauna	Feeding	Egg sac guarding	Additional observations
<i>S. lindborgi</i>	Night and day	Dry limestone forest, rainforest, serpentine forest, urban setting	Under bark, under rocks, in and around houses, in plants	<i>Acacia</i> , Bromeliaceae, <i>Bursera</i> ; <i>Casuarina</i> (Australian pine); <i>Citharexylum</i> , <i>Heliconia</i> , <i>Krugiodendron ferreum</i> (ironwood); <i>Meliococcus bijugatus</i> , <i>Tamarindus indica</i> (Tamarind)	<i>Anolis</i> and <i>Ameiva</i> (lizards); Geckos (var. spp.); Tenebrionidae (darkling beetles); Scorpions; Sparassidae (giant crab spiders); Formicidae (ants); Blattodea (roaches); Isoptera (termites); Centipedes	Isoptera (termites)	No	Being eaten by <i>Anolis</i> (lizard)
<i>S. insularis</i>	Night and day	Along roads, urban, dry forest, agricultural setting	Under bark, on and under rocks, on fences, on trees, in houses	<i>Acacia</i> , <i>Bursera</i> , <i>Casuarina</i> (Australian pine); <i>Cithiarexyum</i> , <i>Coccoloba</i> (Sea Grape); <i>Tamarindus indica</i> (Tamarind)	–	–	Yes	–
<i>S. candidus</i>	Day	Botanic garden, dry limestone forest	Under bark	<i>Bursera</i>	–	–	?	–

Table 2. (Continued.)

Species	Time of day observed	Habitat	Micro-habitat	Plant species on which <i>Selenops</i> was found	Associated fauna	Feeding	Egg sac guarding	Additional observations
<i>S. bani</i>	Day	Dry limestone forest near lake shore below sea level	Under rocks	–	–	–	?	–
<i>S. pensilis</i>	Day	Dry limestone forest near lake shore below sea level	Under rocks	–	–	–	Yes	–
<i>S. marcanoi</i>	Day	Forest near river	Under bark	–	–	–	?	–
<i>S. petrunkevitchi</i>	Day	Altered area near cloud forest – found up to 1250m	Under bark	<i>Eucalyptus</i>	Tettigoniidae (katydid); Onychophoran	–	?	–
<i>S. phaselus</i>	Day and night	Cloud forest, pine forest, human habitation – found from 1400–1566m	Under bark, under rocks, on stone wall at night	–	–	–	?	–
<i>S. simius</i>	Day and night	Urban setting, dry forest, beach	Under bark, under rocks, on rocks at night, in house, In plants	Arecaceae (palms); Bromeliaceae, <i>Coccoloba</i> (sea grape)	–	Blattodea (roach)	?	–
<i>S. cf. geraldinae</i>	Day	Dry forest, beach	Under bark, under rocks, under debris on beach	Arecaceae (palms); Bromeliaceae, <i>Bursera</i>	–	–	Yes	–

single occasion) to prey upon *Selenops* was a conspecific *Selenops*. This occurred when one was disturbed and ran into another larger one, only to be eaten. Also, an adult female of an undescribed species on North Caicos in the Turks and Caicos Islands was found devouring an adult male on a tree at night. The circumstances of this are unknown because when the spiders were encountered, the majority of the male had already been consumed.

In Botucatu, *S. occultus* was observed to feed on roaches and small moths. In the lab, *Selenops* readily accept roaches, crickets, mosquitoes, houseflies and fruitflies. In the Caribbean, *Selenops* have most often been observed feeding on roaches, although they have also been found to feed on termites and other *Selenops*. Gertsch (1949) noted that *Selenops* spiders in Panamá play a significant role in insect control in houses. As *Selenops* spiders do not build webs and sit and wait for their prey, which they capture with amazing speed, it is likely that they primarily consume other nocturnal arthropods that spend significant amounts of time wandering around.

In terms of ecological interactions, the observation of multiple spiders of the same or different species inhabiting the same small area (e.g., a single tree) has important implications in terms of conspecific and congeneric interactions and competition. In terms of evolution, future research will allow us to place the observations documented here within the phylogenetic context of Caribbean species as a whole. It is also interesting to note that although the majority of *Selenops* species in the Caribbean appear to be generalists in terms of microhabitat affinities, multiple speciation events have taken place. This indicates that ecological speciation may not be driving diversification in this group. The data gathered may also have conservation relevance (Dayton 2003; Greene 2005). In particular, habitat destruction is rampant in many areas of the Caribbean and habitats are often thoroughly destroyed before anything is known regarding what occurs in the area in terms of flora and fauna. In heavily touristic islands such as St. Maarten and Providenciales, Turks and Caicos, we have found species new to science and endemic to these island banks, thus providing important information for environmental branches of governments struggling to procure funding or to conserve areas rapidly being lost to development for tourism.

Acknowledgements

We would like to thank the following people for helping us obtain permits or collect spiders for this study: Facundo Franken, Gijs Van Hoorn, Carmabi Institute, Matt Cottam, Mark da Silva, Kelvin Guererro, Renata Platenberg, Arlington James, Steven Toussaint, Inilek Wilmot, Alberto Puente-Rolon, G.B. Edwards, Donna Hamilton, Germain George, Guy Mathurin, Tracey Challenger, Caroline Chaboo, Nicole VanderSal, Greg Pereira, Jim Johnson, Brian Riggs, Andy Caballero, Beverly Mae Nisbeth, Jan den Dulk, Arturo Herrera, Luke Mahler and Eladio Fernandez. We would also like to thank Adriano Kury, José Corronca for the identification of *S. occultus*, Nicole VanderSal for statistical advice, Joe Spagna and two anonymous reviewers for helpful suggestions. This project was funded by the Walker Fund and Keene Forest Entomology Fund, UC Berkeley; the Harriet Exline Frizzell Memorial Fund, CAS; the American Museum of Natural History Theodore Roosevelt Fund; and Sigma Xi.

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