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Spiders (Araneae) of the Everglades National Park, Florida, USA

Michael L. Draney[1], *James W. Berry*[2,*], *and Mia Spaid*[1]

Abstract

The spider fauna of the Everglades National Park in southern Florida was surveyed over 2 widely separated time periods: 1966 to 1967 and 2008 to 2009. Samples were made in 4 of the typical Everglades habitats: sawgrass prairie, willowhead marsh, pineland, and tropical hardwood hammock, as well as several "disturbed" areas. A total of 201 spider species was identified. Twenty-three additional taxa were identified only to genus and included for general Everglades information. One species was documented as new and undescribed, and several others possibly may be new. The Everglades National Park is located at the northern border of the Neotropical ecozone and the southern border of the Nearctic ecozone. Forty-seven percent of the species were Nearctic, 37% Nearctic/Neotropical, 12% Cosmopolitan, and 3% Neotropical. The greatest number of species was collected in the hardwood hammock habitat. Life cycles of 10 common species are provided.

Key Words: ecozone; sawgrass; pineland; hardwood hammock; willowhead marsh; faunistics

Resumen

Se estudió la fauna de arañas del Parque Nacional Everglades en el sur de la Florida durante 2 períodos de tiempo ampliamente separados: 1966 a 1967 y 2008 a 2009. Se tomaron muestras en 4 de los hábitats típicos de los Everglades: pradera de pasto de sierra, pantano de sauce, pinar y madera dura tropical hamaca, así como varias áreas "perturbadas." Se identificó un total de 201 especies de arañas. Se identificaron veintitrés taxones adicionales solo a nivel de género y se incluyeron como una información general sobre los Everglades. Una especie fue documentada como nueva y no descrita mientras que otras posiblemente sean nuevas. El Parque Nacional Everglades está ubicado en el límite norte de la ecozona Neotropical y el límite sur de la ecozona Neártica. El 47% de las especies son del Neártico, 37% del Neártico/Neotropical, 12% cosmopolitanas y 3% Neotropicales. Se recolectó el mayor número de especies en el hábitat de las hamacas de madera dura. Se proporcionan los ciclos de vida de 10 especies comunes.

Palabras Clave: ecozona; pasto de sierra; pinar hamaca de madera dura; pantano de sauce; faunística

The Everglades are now suitable only for the haunt of noxious vermin, or the resort of pestilent reptiles.

Report of Buckingham Smith to the U.S. Senate, 1848 (US Senate 1998 reprint)

The Florida Everglades (Fig. 1) is not a swamp but a slowly moving river, a unique wetland system found nowhere else in the world. Located on the border between Nearctic and Neotropical ecozones, it has a mixture of species from both ecozones. Originally, the Everglades stretched 200 km (120 mi) north to south and 116 km (70 mi) east to west (Caulfield 1970). Today, roughly 60% of the historic area has been lost to development (Lodge 2005).

The noted Florida journalist and eminent conservationist Marjorie Stoneman Douglas (1947) coined the term "river of grass," and it has been used widely since. The Everglades ecosystem owes its characteristics to several features, the first of which is its limestone bedrock. Called the Hawthorne Formation, this bedrock is an impermeable layer of clay that effectively blocks the Everglades rainfall above it from aquifers that exist in lower bedrock layers. Coupled with sparse connections to rivers or lakes, the Hawthorne Formation forces the Everglades to receive water primarily from rainfall. As a result, the Everglades is the only known wetland that is composed primarily of flowing sheet waters. The waters that move through the Everglades discharge to both the Atlantic Ocean and the Gulf of Mexico (Lodge 2005).

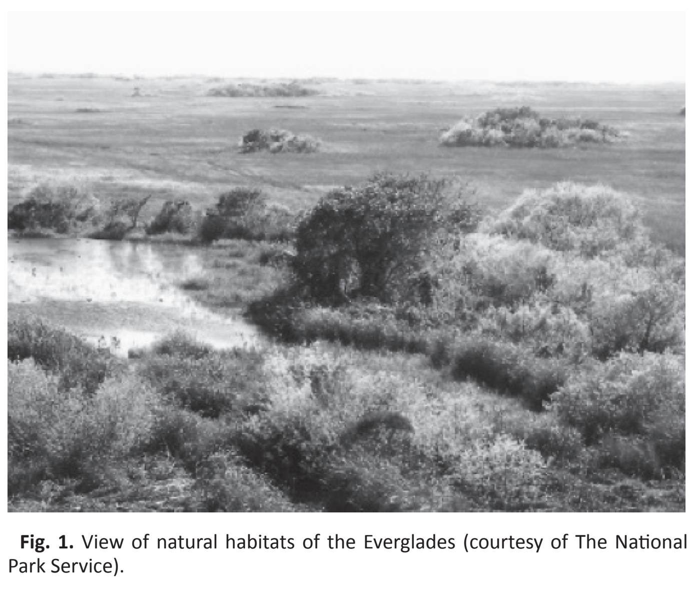

Fig. 1. View of natural habitats of the Everglades (courtesy of The National Park Service).

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The Everglades' geographical location is the second fundamental trait, because it puts the region on the border of northern temperate and southern subtropical Caribbean climates. Annual wet and dry seasons are the primary agent of change, as opposed to the summer/winter cycles usually seen in the rest of eastern North America. As a result, the region displays a unique mix of temperate and tropical habitats that is home to both North American and Caribbean species. Coupled with 5,000 yr of peat soil buildup, the climate allows for a great diversity of organisms to coexist in the following recognized communities: upland, which includes pinelands and tropical hardwood hammocks; and freshwater wetland, which includes tree islands, sawgrass marshes, wet prairies, slough, and land-bound waterways such as creeks (Duever 1994; Gunderson 1994; Lodge 2005). In addition to those inland communities there are saltwater mangrove and coastal habitats that may be included (Lodge 2005).

The upland forests of tropical hardwood hammock and pine tend to be found on more xeric soils, including bare limestone. They were found formerly throughout south Florida, but due to human developments they have been reduced to 10% of their original range, all of which is protected currently within the Everglades National Park (National Park Service 2013).

Fire is the primary determinant of forest type in the upland sites. Hardwood hammocks can form dense and diverse tree stands of primarily West Indian evergreen tree species. Pinelands, in contrast, are maintained by regular outbreaks of fire every 5 to 10 yr. This creates a canopy of fire-resistant south Florida slash pines (*Pinus elliotti* var. *densa* Engelm.; Pinaceae). Pinelands with longer fire intervals have a denser understory of hardwood hammock species, whereas shorter fire intervals create a sparse understory and more open canopy (Gunderson 1994; Lodge 2005).

In contrast, wetland communities found at lower elevations are able to tolerate standing waters and floods for at least part of the yr. Tree islands, such as cypress and willow stands, are forest communities dominated by their namesake trees, and may be found at higher elevations. Herbaceous wetland communities, in contrast, tend to be categorized by whether they are on marl or peat soils. Marl tends to be drier and found in higher elevations in the south, whereas peat is lower and wetter in the central Everglades region. Sawgrass (*Cladium* sp. P. Brown; Cyperaceae) communities are an exception, as they can form large, dense, monospecific stands that are well-suited to survive floods, fire, and low nutrient soils. Sawgrass (a sedge) is so common that it is the defining plant species of the Everglades (Gunderson 1994; Lodge 2005).

For most of its existence the Everglades was maintained by natural events such as storms and fire, with minimal human modifications until Europeans arrived. After the Seminole Indian wars of the 1840s removed most of the indigenous peoples, plans for canals and roads to support growing towns were carried out, modifying much of the Everglades before anyone could record a comprehensive pre-disturbed map or description of it. The primary goals of these modifications were to lower the water level, "drain the swamp," to reveal more dry land and gain better control over floods to stabilize agricultural land (Lodge 2005). For many, this goal still exists.

The first of these projects occurred in 1881, when Hamilton Disston was granted land by the US Federal Government in exchange for draining the waters of Lake Okeechobee to open up more land for development. He had a canal dug from the west side of the lake to the Caloosahatchee River, connecting Lake Okeechobee to the Gulf of Mexico and allowing passage of steamboats from the Gulf to the Lake. He intended to continue his work by excavating additional canals, but ran into financial and environmental problems that stopped him in 1893 (Lodge 2005).

The Federal Government picked up in the early 1900s where Disston left off. Four additional canals to further drain Lake Okeechobee were built by 1917, and a canal connecting the lake to the Atlantic was completed by 1926. As planned, these canals prompted population growth by controlling the floodwaters better and allowing a system of navigation from the ocean and Gulf. The US Army Corps of Engineers created additional canals and dikes in the 1930s.

Natural disasters interfered with the plans, and several major storms damaged the canals and dikes severely, including 2 hurricanes that killed over 2,000 people through flooding. Additional storms that occurred after the 1930s projects were completed continued to flood towns and roads for wk at a time, disrupting local businesses. Starting in 1948, modifications to existing canals were made to withstand such dangerous floods, along with additional channel and weir structures. As a result, waters no longer flooded and receded according to the seasons; instead they were directed by human technologies. Vast tracts of wetland were destroyed to provide agricultural fields and residential areas. What natural area remained existed as fragmented landscapes, divided by roads, canals, and buildings (Lodge 2005).

These modifications reduced the Everglades to approximately 40% of its known historic area (Lodge 2005) and placed the remaining ecosystem under great stress. Migratory birds depend on the Everglades as a breeding site, and permanent residents, such as mammals and reptiles, find refuge through the Everglades' protected status as a national park. The fresh water filtering through the Everglades is a critical resource for the entire south Florida region because often it is the sole source of fresh water for recreational, home, and agricultural use.

Starting in the 1990s, several major plans were enacted at all levels of government to restore the system as close to historic forms as possible within the current spatial constraints and human demands. Federal and state plans focused primarily on the water systems, whereas more local plans focused on a variety of restoration projects.

The main objective of this research was to obtain a comprehensive (though undoubtedly not complete) list of spiders of the Everglades National Park, and we also present some basic biological information for species abundant enough to estimate seasonal and habitat distribution. The 2 widely separated sampling periods (1960s and 2000s) (Fig. 2) provide 2 types of "baseline" data. The 1960s sampling occurred not only 4 decades prior to the latter sampling, but also before much of the Everglades restoration projects undertaken by the National Park Service and Army Corps of Engineers started in the 1970s (Grunwald 2006). This baseline data will become more valuable during this century as the entire ecosystem is threatened by sea level rise (Dessu et al. 2018; NOAA 2018). The Everglades has a low elevation, only 2.44 m (8 ft) above sea level at the highest point with an average elevation of 1.83 m (6 ft), and is flat throughout the park. With the latest predictions regarding rising sea levels at 2 m (6.56 ft) in this century alone, much of the Everglades will soon be permanently submerged, assuming no human-created barriers are built.

No species list for spiders in any Everglades habitat has yet been published. Stewart Peck (Carlton University, Ontario, Canada) deposited in the American Museum of Natural History about 21 salticid species collected from the park during a 1986 insect survey. The few Everglades spider studies that have been published focused on a particular species or clade rather than the regional diversity (Jones & Parker 2002).

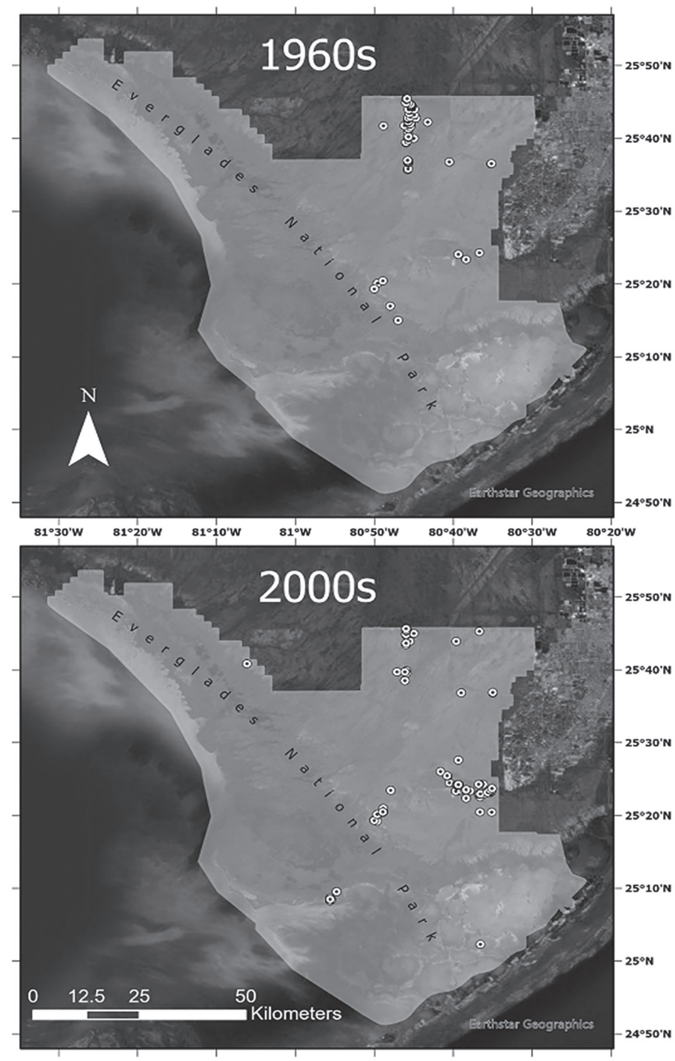

Fig. 2. Map of Everglades National Park showing spider sampling locations in the 1960s (above) and 2000s (below).

Materials and Methods

James W. Berry had an opportunity to survey the spider population in the Everglades National Park in 1966 to 1967, but taxonomic work was not completed or published then. Berry again was able to collect in the park in 2008 to 2009 when Elizabeth R. Berry joined him as a collector. Sampling locations during the 2 time periods (1960s and 2000s) are shown in Figure 2.

In 1966 to 1967, GPS and other digital devices for geospatial location were not available to the collector, so sites were measured from known points by automobile odometer where roadways accessed the sites (approximate GPS coordinates were estimated later by the authors). Remote sites were identified by names on maps where named sites were used. Two sets of sites were used in both collecting periods. On the north side of the park: Shark River Slough; on the south side of the park: Main Gate entrance south to Flamingo. From the Shark River Slough to the Main Gate is measured as 63 km (38 mi) and from the Main Gate to Flamingo is measured as 83 km (50 mi).

On the north side of the park at the Shark River Slough is a 25 km (15 mi) loop road. In 1966 to 1967 the road was open to the public, but in 2008 to 2009 the traffic flow had been reversed and the entire roadway closed to the public except for tourist trams and bicycles. All the Shark River Slough sampling sites in both collecting periods were accessible by the loop road and included hammocks, willowheads, and vast areas of sawgrass. Because of roadway changes over 40 yr, it was virtually impossible to be certain of collecting identical sites both times. Acceptable and approximate locations were established. The same types of sites were used, not necessarily the same sites. In 2008 to 2009, we sampled as much in daylight hours as we could, then after dark we used paved and boardwalk trails for collecting by headlamp. Other sites were too dangerous for after-dark foot travel.

On the south side, sites used were primarily those identified by names on maps (Gumbo Limbo Trail, Mahogany Hammock). Daylight and after-dark collecting methods were the same as those used on the north side in each of the time periods.

Sampling methods in 1966 to 1967 were different from those in 2008 to 2009 because conditions changed. The earlier methods included twice-monthly samples at each site, including (1) samples with a heavy-duty sweep net with 200 sweeps per site; (2) litter searches of a square meter plot, down to mineral substrate; and (3) other non-quantitative techniques such as tree shaking and hand-collecting. An airboat was available in 1966 to 1967. As the airboat moved through the sawgrass, spiders (primarily *Tetragnatha* L.; Araneae: Tetragnathidae spp.) were swept into the boat by the hundreds and hand caught. Other specimens were individually hand caught on land.

In 2008 to 2009 other methods were used. The airboat was available only to park staff meaning that a primary technique for sampling sawgrass was lost, and some collecting sites could not be reached by any other means. Collecting trips were reduced to once monthly, and while sweeping techniques remained the same, litter collection was more extensive, and night collecting (using a head lamp) was added on dry land to capture specimens at head-high levels, primarily orb weavers, and ground level specimens (lycosids) because of their reflective eyes.

Unfortunately, collecting differences outlined above completely eliminated any attempts at quantitative sampling. Access to the park was sometimes unavailable in both time periods because of natural disasters such as hurricanes, flooding, wildfire, or administrative decisions. It should be noted that at this writing, the north side is closed because of flooding.

Specimens were preserved in 70% ethanol, and identifications were made primarily by Joseph A. Beatty, G. B. Edwards, Herb Levi, Michael Draney, and Mia Spaid. As a consistency measure, specimens of all identified taxa were confirmed by the first author (MD). As required by federal law, all specimens are deposited in the South Florida Collections Management Center at The Everglades National Park in Homestead, Florida, USA.

The biogeographic status of each species was based upon the authors' judgment and data available in the World Spider Catalog (version 20) (2019). Various species were selected for plotting abundance and seasonal distribution where numbers were large enough (more than 100 total individuals collected) to permit manipulation of the data. An exception is *Schizocosa floridana* Bryant (Araneae: Lycosidae) which is represented by a smaller total number of individuals collected, but is a species known to occur only in Florida (Stratton 1997). Because of limited collecting, the distribution given in Table 1 may not represent the true distribution of the species, and our judgment in assigning ecozones may be premature.

We identified 4 species whose seasonality was well-known from farther north in the piedmont of North Carolina (Berry 1967, 1970) and abundant enough in the present samples to attempt a seasonal comparison of populations from the 2 locations (Fig. 3). All specimens were collected by the same person (James Berry) using similar techniques. The North Carolina specimens were made available for re-study by the Florida State Collection of Arthropods in Gainesville, Florida, USA.

Table 1. Spider species found in The Everglades National Park. The first column lists species by family. The second column lists habitat(s) where a species was most abundant, based on the current collection: H = hardwood hammock, P = pinelands, S = sawgrass, W = willowhead, M = mangrove, and D = disturbed. The third column lists ecozone assignment based on data from The World Spider Catalog (Version 20) (2019) and the authors' judgment: NA = Nearctic, NT = Neotropical, and C = cosmopolitan. The fourth column shows the number of individuals collected in each era noted as 1960s or 2000s. Taxa denoted as "sp." were not identifiable either due to taxonomic difficulty (*Opopaea*, *Psilochorus*) or to lack of adult specimens (all other taxa); taxa denoted as "*cf*." are hypothesized to belong to as-yet-undescribed new species. [a] = Taxa understood to be non-native, introduced species.

AGELENIDAE			
Agelenopsis sp.	P	NA	0/7
Barronopsis sp.	S	NA/NT	3/0
ANYPHENIDAE			
Arachosia cubana (Banks)	S, W	NT	11/0
Hibana velox (Becker)	H, W	NA/NT	112/15
Oxysoma sp.	P	?	0/1
Wulfila albens (Hentz)	H, P	NA	1/9
Wulfila wunda Platnick	H	NA/NT	0/1
ARANEIDAE			
Acacesia hamata (Hentz)	P, H	NA/NT	0/21
Acanthepeira cherokee Levi	D	NA	0/4
Acanthepeira venusta (Banks)	S	NA/NT	29/1
Allocyclosa bifurca (McCook)	H, P	NA/NT	0/7
Araneus bonsallae (McCook)	P	NA	0/7
Araneus miniatus (Walckenaer)	H	NA	13/3
Araneus pegnia (Walckenaer)	H	NA/NT	23/1
Argiope aurantia Lucas	H	NA/NT	8/0
[a]*Argiope trifasciata* (Forsskål)	P	NA/NT	3/3
Cyclosa turbinata (Walckenaer)	P	NA/NT	3/1
Cyclosa walckenaeri (O. Pickard-Cambridge)	M	NA/NT	0/4
Eriophora ravilla (C.L. Koch)	H, W	NA/NT	2/52
Eustala anastera (Walckenaer)	P	NA/NT	0/12
Eustala cepina (Walckenaer)	W, H	NA	7/26
Eustala eleuthera Levi	H	NA/NT	0/1
Eustala sp.	H	NA	21/30
Gasteracantha cancriformis (Linnaeus)	H	NT	0/1
Gea heptagon (Hentz)	H, P	NA/NT	1/1
Hypsosinga pygmaea (Sundevall)	D	NA	0/2
Larinia directa (Hentz)	P, S	NA/NT	2/14
Larinioides cornutus (Clerck)	S	NA	39/0
Mangora gibberosa (Hentz)	P	NA	10/57
Mangora placida (Hentz)	P, H	NA	0/14
Mangora spiculata (Hentz)	P, H	NA	7/65
Mecynogea lemniscata (Walckenaer)	P, H	NA/NT	2/5
Metepeira labyrinthea (Hentz)	P, W	NA	1/2
Metazygia wittfeldae (McCook)	H, W	NA/NT	2/7
Metazygia zilloides (Banks)	H, W	NA/NT	128/32
Micrathena sagittata (Walckenaer)	H	NA/NT	1/0
Neoscona arabesca (Walckenaer)	W	NA/NT	8/65
Neoscona crucifera (Lucas)	W	NA	0/1
Neoscona domiciliorum (Hentz)	H, W	NA	2/3
Neoscona pratensis (Hentz)	S, W	NA	10/431
Scoloderus sp.	W	NA	1/0
Verrucosa arenata (Walckenaer)	H	NA/NT	0/19
Wagneriana tauricornis (O. Pickard-Cambridge)	H	NA/NT	25/31
CHEIRACANTHIIDAE			
Cheiracanthium inclusum (Hentz)	P, H	NA/NT	0/14
CLUBIONIDAE			
Clubiona abboti (Koch)	H	NA	5/0
Clubiona catawba Gertsch	P	NA	0/2
Clubiona cf. quebecana Dondale & Redner	W	NA	0/2
Clubiona kiowa Gertsch	D	NA	0/1
Clubiona maritima L. Koch	S	NA/NT	2/0
Clubiona procteri Gertsch	S	NA	4/0
Clubiona saltitans Emerton	P	NA	0/1
Elaver excepta (L. Koch)	H	NA/NT	0/6

Table 1. (Continued)

CORINNIDAE			
Castianeira floridana (Banks)	H	NA/NT	1/0
Castianeira longipalpus (Hentz)	W	NA	0/1
CTENIDAE			
Ctenus sp.	P	C	0/1
DEINOPIDAE			
Deinopis spinosa Marx	H	NA/NT	2/0
DICTYNIDAE			
Dictyna volucripes Keyserling	W	NA	1/0
Emblyna altamira (Gertsch & Davis)	S	NA/NT	18/0
Emblyna coweta (Chamberlin & Gertsch)	H	NA	26/1
Emblyna cruciata (Emerton)	W	NA	11/0
Emblyna florens (Ivie & Barrows)	H	NA	76/4
Emblyna manitoba (Ivie)	H, S	NA	11/6
Emblyna sublata (Hentz)	?	NA	4/0
Emblyna sublatoides (Ivie & Barrows)	S, W	NA	8/2
Lathys albida Gertsch	D	NA	0/1
GNAPHOSIDAE			
Callilepsis imbecilla (Keyserling)	P	NA	0/4
Camillina pulchra (Keyserling)	W	NA/NT	1?/2
Cesonia bilineata (Hentz)	D, H	NA	1/1
Drassylus eremitus Chamberlin	H	NA	2/2
Drassylus orlando Platnick & Corey	H	NA	0/2
Litopyllus sp.	H	NA/NT	2/0
Micaria cf. elizabethae Gertsch	D	NA	0/5
Micaria elizabethae Gertsch	D	NA	0/1
Sergiolus unimaculatus Emerton	S	NA	7/0
HAHNIIDAE			
Hahnia cinerea (Emerton)	H	NA	0/3
LINYPHIIDAE			
Agyneta cf. barrowsi (Chamberlin & Ivie)	?	NA	0/2
Agyneta fabra (Keyserling)	D	NA	0/1
Agyneta micaria (Emerton)	D	NA	0/7
Agyneta parva (Banks)	H	NA	2/6
Agyneta picta (Chamberlin & Ivie)	H	NA	0/12
Agyneta regina (Chamberlin & Ivie)	P	NA	0/1
Agyneta cf. serrata (Emerton)	H	NA	0/1
Agyneta serrata (Emerton)	H	NA	2/1
Ceraticelus creolus Chamberlin	W	NA	1/0
Ceraticelus emertoni (O. Pickard-Cambridge)	P, S	NA	6/2
Ceraticelus pygmaeus (Emerton)	W	NA	1/0
Ceratinella brunnea (Emerton)	?	NA	1/0
Ceratinopsis nigripalpis Emerton	S	NA	1/0
[a]*Erigone autumnalis* Emerton	?	C	2/0
Erigone barrowsi Crosby & Bishop	D	NA/NT	0/1
Erigone dentigera O. Pickard-Cambridge	D	C	0/9
Florinda coccinea (Hentz)	H, W	NA/NT	2/0
Grammonota cf. vittata, inornata	S	NA	4/0
Grammonota vittata Barrows	S	NA	16/9
Graphomoa theridioides Chamberlin	H	NA	0/41
Mermessus dentiger O. Pickard-Cambridge	?	NA/NT	1/0
Mermessus maculatus (Banks)	H	C	3/12
LYCOSIDAE			
Allocosa furtiva (Gertsch)	D	NA	0/3
Gladicosa bellamyi (Gertsch &Wallace)	H	NA	0/7
Hogna helluo (Walckenaer)	D	NA	0/1
Hogna lenta (Hentz)	D	NA	0/2
Hogna miami (Wallace)	P	NA	0/7
Pardosa floridana (Banks)	H	NA/NT	29/0
Pirata appalacheus (Gertsch)	H	NA	0/12

Table 1. (Continued)

Pirata insularis (Emerton)	H	C	0/9
Rabidosa sp.	P	NA	0/2
Schizocosa floridana Bryant	H	NA	76/0
Tigrosa annexa (Chamberlin & Ivie)	H	NA	0/3
Tigrosa georgicola (Walckenaer)	H	NA	2/1
[a]*Trochosa ruricola* (DeGeer)	D	C	0/45
MIMETIDAE			
Mimetus interfector Hentz	H	NA	1/4
Mimetus nelsoni Archer	H	NA	1/0
Mimetus notius Chamberlin	P	NA	0/11
Mimetus syllepsicus Hentz	H	NA	149/2
OECOBIIDAE			
Oecobius concinnus Simon	D	NT	0/1
OONOPIDAE			
Opopaea sp.	?	C	4/0
Gamasomorpha lutzi (Petrunkevitch)	H, D	NA/NT	0/5
Heteroonops spinimanus (Simon)	H	C	8/16
Ischnothyreus peltifer (Simon)	H	C	0/20
Orchestina nadleri Chickering	D	NA/NT	0/1
Scaphioides minuta (Chamberlin & Ivie)	H	NA	15/0
Triaeris stenaspis Simon	?	C	0/25
OXYOPIDAE			
Oxyopes acleistus Chamberlin	P	NA	0/10
Peucetia viridans (Hentz)	P	NA/NT	0/9
PHILODROMIDAE			
Philodromus placidus Banks	H, S	NA	63/0
Tibellus maritimus (Menge)	S	C	103/8
PHOLCIDAE			
[a]*Crossopriza lyoni* (Blackwall)	D	C	0/8
Modisimus sp.	D	?	8/1
Physocyclus globosus (Taczanowski)	D	C	0/1
Psilochorus sp.	D	NA	0/2
PHRUROLITHIDAE			
Phrurotimpus borealis (Emerton)	?	NA	1/0
Phrurotimpus cf. illudens Gertsch	?	NA	0/2
Phrurolithus emertoni Gertsch	H	NA	31/0
PISAURIDAE			
Dolomedes triton (Walckenaer)	H, W	NA/NT	179/14
Pisaurina undulata (Keyserling)	S, W	NA/NT	203/76
SALTICIDAE			
Admestina archboldi Piel	D	NA	1/0
Anasaitis canosa (Walckenaer)	D, P	NA	4/2
Cheliferoides longimanus Gertsch	W	NA	1/0
Colonus puerperus (Hentz)	P	NA	0/1
Colonus sylvanus (Hentz)	H	NA/NT	179/2
Eris flava (Peckham & Peckham)	S	NA/NT	298/3
Hentzia grenada (Peckham & Peckham)	S	NA/NT	221/10
Hentzia mitrata (Hentz)	H, W	NA/NT	66/3
Hentzia palmarum (Hentz)	W, H	NA/NT	197/55
Lyssomanes viridis (Walckenaer)	H	NA	265/21
Maevia sp.	P	NA	4/0
Marpissa bina (Hentz)	S	NA	7/0
Marpissa pikei (Peckham & Peckham)	S, P	NA/NT	4/0
Menemerus bivitattus (Dufour)	D	C	0/5
Neonella camillae Edwards	P	NT	0/1
Neonella vinnula Gertsch	P, D	NA	0/2
Paramaevia hobbsi (Barnes)	P	NA	0/4
Pelegrina galathea (Walckenaer)	P	NA/NT	0/1
Phidippus audax (Hentz)	S, W	NA	2/0

Table 1. (Continued)

Phidippus clarus Keyserling	P	NA	0/1
Phidippus regius C.L. Koch	P	NA/NT	0/25
Synageles noxiosus (Hentz)	P, S, H	NA/NT	1/8
Synemosyna petrunkevitchi (Chapin)	H	NA/NT	1/0
Zygoballus rufipes Peckham & Peckham	H	NA/NT	18/2
Zygoballus sexpunctatus (Hentz)	P	NA	0/48
SCYTODIDAE			
Scytodes fusca Walckenaer	W, H	C	0/7
Scytodes thoracica (Latreille)	P, H	C	0/14
TETRAGNATHIDAE			
Dolichognatha pentagona (Hentz)	H	NA/NT	2/1
Glenognatha foxi (McCook)	S	NA/NT	23/2
Leucauge argyra (Walckenaer)	H, W	NA/NT	78/84
Leucauge venusta (Walckenaer)	H	NA	92/103
Trichonephila clavipes (Linnaeus)	H	NA/NT	75/3
Pachygnatha calusa Levi	M, W	NA	12/0
Tetragnatha caudata Emerton	S, H	NA/NT	270/14
Tetragnatha elongata Walckenaer	H, W	NA/NT	0/45
Tetragnatha extensa (Linnaeus)	H	C	0/2
Tetragnatha gracilis (Bryant)	P	NA/NT	?
Tetragnatha guatemalensis O. Pickard-Cambridge	H, W	NA/NT	155/94
Tetragnatha pallescens O. Pickard-Cambridge	S	NA/NT	561/65
Tetragnatha tropica O. Pickard-Cambridge	H	NT	?
Tetragnatha vermiformis Emerton	S	C	8/0
Tetragnatha versicolor Walckenaer	H	NA/NT	108/12
THERIDIIDAE			
Anelosimus studiosus (Hentz)	W, H	NA/NT	247/32
Argyrodes elevatus Taczanowski	H, W	NA/NT	0/7
Argyrodes nephilae Taczanowski	S, H	C	39/12
Coleosoma acutiventer (Keyserling)	W	NA/NT	3/16
Dipoena nigra Emerton	H	NA	22/0
Emertonella taczanowskii (Keyserling)	H	C	6/0
Episinus amoenus Banks	H	NA	3/15
Faiditus americanus (Taczanowski)	H, W	NA/NT	110/10
Faiditus caudatus (Taczanowski)	H	NA/NT	0/25
Faiditus globosus (Keyserling)	H	NA/NT	5/5
Henziectypus conjunctus (Gertsch & Mulaik)	P, W	NA	0/2
[a]*Meotipa pulcherrima* (Mello-Leitao)	H, P	C	0/40
Neospintharus furcatus (O. Pickard-Cambridge)	H	NA/NT	7/0
Neospintharus *trigonum* (Hentz)	P	NA	0/11
Phycosoma lineatipes (Bryant)	H	NA/NT	0/2
Phylloneta pictipes (Keyserling)	H	NA	6/1
Platnickina mneon (Bosenberg & Strand)	H	C	1/3
Rhomphaea projiciens O. Pickard-Cambridge	H	C	0/24
Spintharus flavidus Hentz	H	NA/NT	10/86
Stemmops bicolor O. Pickard-Cambridge	H	NA/NT	46/1
Theridion cf. fungosum (Keyserling)	D	NA/NT	0/3
Theridion cf. goodnightorum Levi	D	NA	2/0
Theridion cf. *sexpunctatum* (Emerton)	?	NA	0/2
Theridion flavonotatum Becker	W, H	NA/NT	80/15
Theridion glaucescens Becker	W, H	NA	54/2
Theridion goodnightorum Levi	?	NA	?
Theridion myersi Levi	D	NA/NT	0/4
Theridula gonygaster (Simon)	W	C	1/0
Thymoites expulsus (Gertsch & Mulaik)	H	NA/NT	1/0
Thymoites unimaculatus (Emerton)	H	NA	3/0
Tidarren haemorrhoidale (Bertkau)	?	NA/NT	1/0
Tidarren sisyphoides (Walckenaer)	H	NA/NT	3/6
Wamba sp.	D	NA/NT	0/1
Yunohamella lyrica (Walckenaer)	H	NA	1/24

Table 1. (Continued)

THOMISIDAE			
Bassaniana sp.	?	NA	0/1
Mecaphesa celer (Hentz)	P, H	NA/NT	1/11
Misumenops bellulus (Banks)	P, D	NA/NT	51/141
Misumessus oblongus (Keyserling)	W, P	NA	6/6
Synema sp.	P	C	0/3
Tmarus rubromaculatus Keyserling	H	NA	17/18
Xysticus discursans Keyserling	D	NA	0/4
TRACHELIDAE			
Trachelas similis O. Pickard-Cambridge	H	NA/NT	32/7
ULOBORIDAE			
Uloborus campestratus Simon	H	NA/NT	0/10
Uloborus glomosus (Walckenaer)	H	NA	0/35
ZODARIIDAE			
Zodarion berryi Bosmans & Draney	D	NA	0/4

Results

From our collection of over 10,000 specimens, we identified 201 species. An additional 23 taxa were identified only to genus, either because no mature specimens were collected, or because taxonomists had reservations about the species of the specimens, but we include them in the total 224 reported taxa as listed in Table 1.

We found 81 species principally in hardwood hammocks, and 47 species in pineland habitat. The sawgrass habitat yielded 22 species. The smallest number of species, 21, was found in willowhead communities. These low numbers for sawgrass and willowhead are not surprising. Sawgrass presents as a monoculture, and the total area occupied by willowhead is much less than the other habitats, plus there is no significant litter fauna in willowhead marshes. We also collected 20 species primarily in a number of disturbed habitats that included roadsides, parking lots, abandoned structures, and the park's landscape rubbish pile. Primary habitat could not be determined for 10 species due to incomplete collecting labels, and 2 species were collected from the edge of mangrove sites.

LIST OF SPECIES

The list, Table 1, shows specific name, principal habitat(s), and ecozone for each species. Note that some morphospecies could not be identified to the species level due to the lack of adult specimens, and those identified as *Opopaea* Simon (Araneae: Oonopidae) and *Psilochorus* Simon (Araneae: Pholcidae) could not be confidently identified due to difficult taxonomy. The primary habitat is listed first. We also listed the second most prominent habitat for a species, if the primary habitat had the largest number of individuals captured and secondary habitat closely approximated it, e.g., *Hentzia palmarum* (Hentz) (Araneae: Salticidae) W, H.

For each species, we described each taxon as having either a Nearctic, Neotropical or Cosmopolitan distribution based on the World Spider Catalog (version 20) (2019). Because of limited collecting, the distribution given may not represent the true distribution of the species, and our judgment may be premature. Some species have a distribution given in the World Catalog such as "North America & Venezuela," most clearly not the whole picture, so our judgment may be in error, but represents the best-known evidence to date. Using our ecozone assignment, 47% of species collected were Nearctic, 37% both (Nearctic/Neotropical), 12% Cosmopolitan, and 3% Neotropical. Ten species could not be assigned an ecozone because of incomplete label data.

SEASONAL LIFE CYCLES

Although the Everglades spiders were not collected using quantitative sampling, we have attempted to determine the life cycles of 10 species (Fig. 4a-j), but it is obvious that any attempt to describe the seasonal distribution of these species is an extremely artificial undertaking. Some species overwinter as adults, others as juveniles or eggs; conversely, others are wet-season species. Still others are found throughout the yr. It is commonly known that sometimes there are great fluctuations in the populations of different species in different yr. It is assumed that climatic conditions may be responsible for these observations. Since a seasonal graph was not determined for each of the major habitats, it is not known how the populations of the 4 habitat types fluctuate.

Metazygia zilloides (Banks) (Araneae: Araneidae; Fig. 4a), a small, nocturnal orb-weaver was taken predominantly in hammocks by sweeping in the 1960s and by sweeping and night-lighting in the 2000s collecting periods.

Anelosimus studiosus (Hentz) (Araneae: Theridiidae; Fig. 4b) adults are found throughout the yr in the Everglades. Juveniles were found in every mo with peaks in Mar to Apr. Specimens have been found from New England to Texas and south to Florida. *Anelosimus studiosus* has a true Nearctic distribution, inhabiting bushes and trees, most often in the Everglades in willowheads and small hammocks. It was not found in sawgrass. Almost all *Anelosimus* specimens were found in the northern half of the Everglades National Park: 90% in the northern part, 10% in the southern part. Similarly, 90% of specimens were found in the 1966 to 1967 collection and about 10% in 2009. We found no obvious reason for this distribution. Almost all specimens were taken by sweeping.

Hibana velox (Becker) (Araneae: Anyphenidae; Fig. 4c) adults and juveniles are found throughout the yr in the South (Gulf Coast and Florida). In the Everglades National Park, they are found primarily on the north side of the park in small, isolated hammocks and in willowhead depressions (shallow prairie with willows).

It is difficult to get an accurate count of lycosid species because there are many immature specimens, and with several species, taxonomists often could not determine which immatures were in which species. Adult *Schizocosa floridana* (Uetz & Dondale) (Araneae: Lycosidae; Fig. 4d) were found in late summer. Found in the US only in Florida, it is also known from Northern Africa, the Middle East, and Australia, and was very likely introduced to locations outside North America, given the distribution of members of its genus (World Spider Catalog [Version 20] 2019). It was collected in hardwood hammocks in litter.

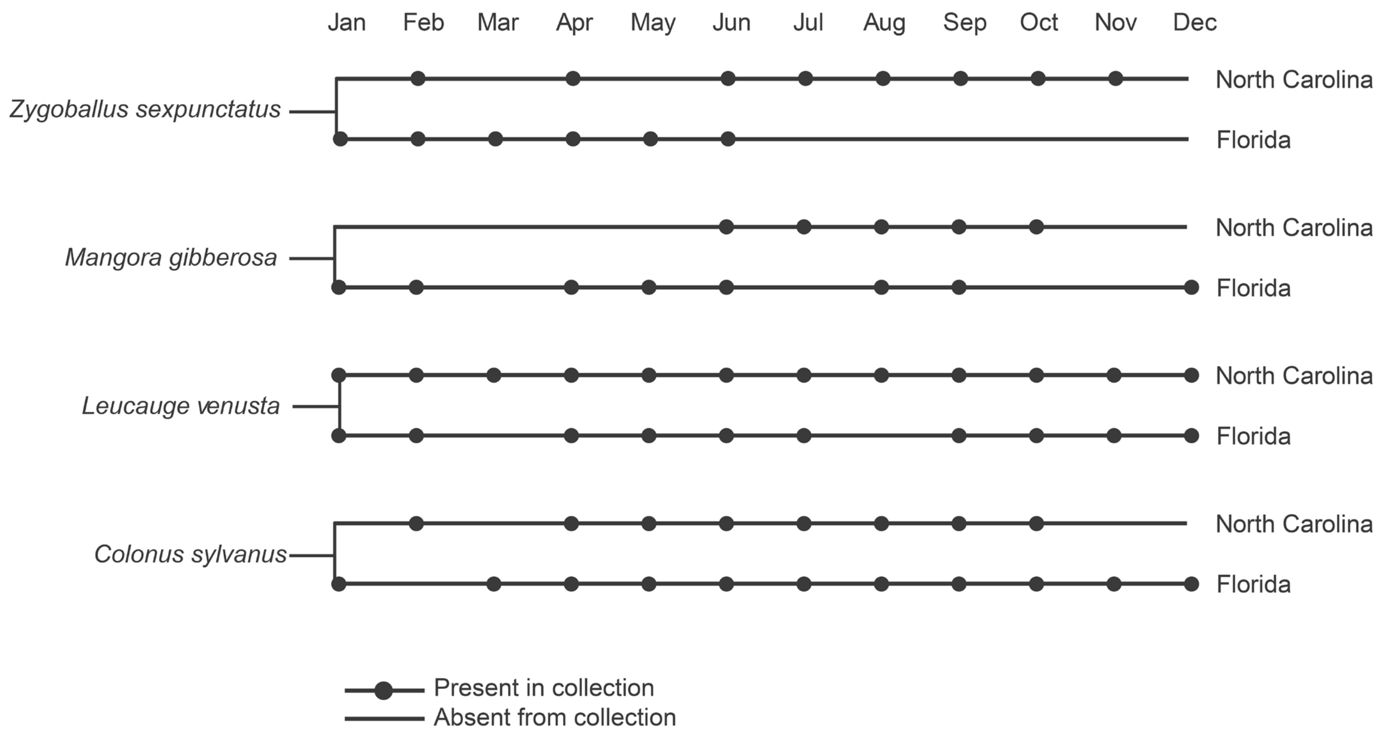

Fig. 3. Comparison of the seasonal difference in 4 Nearctic species found in both the Everglades and 1,500 km further north in North Carolina.

Misumenops bellulus (Banks) (Araneae: Thomisidae; Fig. 4e), a colorful crab spider, is found in the US, Virgin Islands, and Cuba; therefore, its probable distribution is Nearctic/Neotropical. It inhabits dry meadows and sunny forests. In the Everglades, it is found in pinelands, willowheads, and sawgrass primarily in the northern half of the Everglades Park. Adults and juveniles are found throughout the yr and were most abundant in the Aug collections.

Faiditus americanus Taczanowski (Araneae: Theridiidae; Fig. 4f) is found primarily in the northern parts of the park (Shark River Slough). This species, found mostly in shrubs, is present throughout the yr. It is puzzling that it is found in 38 sites on the north side of the park and only 6 sites on the south side; this represents a distance of about 85 km from northern sites to southern ones. We observed the same distribution pattern in *A. studiosus* above.

Hentzia palmarum (Hentz) (Araneae: Salticidae; Fig. 4g) is distributed widely over the eastern US, in the Caribbean, and Central America to Honduras. It is found predominantly in willowhead and hammock habitats in the Everglades, but it is found also in the pinelands.

Mimetus syllepsicus Hentz (Araneae: Mimetidae; Fig. 4h) presents an unusual seasonal distribution. In the Everglades the preponderance of specimens, both adult and juvenile, was captured by sweeping in the month of May. Specimens were taken by the same collector using the same sweeping technique during daylight hours at the same collecting sites mo after mo. Inspection of the same collector's records for *M. syllepsicus* captured in North Carolina revealed a similarly unusual distribution. In North Carolina the preponderance was taken in the mo of Sep (Berry 1970).

Tetragnatha guatemalensis O. Pickard-Cambridge (Araneae: Tetragnathidae; Fig. 4i) adults and immatures were found in or near small hammocks and willowheads, and in disturbed areas in the Shark River Slough. The species generally is present throughout the yr with peaks of immatures in late summer and fall.

Lyssomanes viridis (Walckenaer) (Araneae: Salticidae; Fig. 4j) is a translucent, brilliant green spider, commonly known as the Magnolia Green Jumping Spider (Edwards & Marshall 2001). In the Everglades it usually is seen yr-round, and 95% of the specimens were found in mahogany hammocks. Most members of the genus are tropical, but 6 species are found in southeastern US (Nearctic).

DISTRIBUTION BY HABITAT

One would expect some species to be found in great abundance in some habitats while almost totally absent from others. For example, *Leucauge argyra* (Walckenaer) (Araneae: Tetragnathidae) was absent from the collection in sawgrass, but abundant in hardwood hammocks. Because samples varied so much (depending upon numerous environmental factors), listed in Table 2 are the 6 most abundantly collected species from each habitat type.

We compared the species found in the 4 habitats examined and determined the degree of similarity within the 4 groups. As expected, the greatest difference in the 4 habitats was between sawgrass and pineland (only 14 species in common). The most similar faunal groups were those in pineland and hardwood hammock (86 species in pinelands, 133 species in hardwood hammocks with 51 species in common). Sorensen analysis, a calculation of the proportion of total species in 2 habitats that are common to both (Table 3) supports these comparisons. These numbers do not include those species found only in disturbed areas (roadside, landscape trash piles, structures, and mangrove).

We attempted to determine comparative life cycles of 4 species commonly found both in the Everglades and in the Piedmont region of North Carolina (Berry 1967, 1970) – some 1,500 km further north – to see if the southern specimens' life cycles correlated to the warmer, longer Everglades growing season, and the more northerly specimens correlated with their shorter "summer" season (Fig. 3). There were differences in seasonal life cycle of *Mangora gibberosa* (Hentz) (Araneae: Araneidae), with the northern specimens largely absent from the collection in the winter mo. An opposite pattern was displayed by *Zygoballus sexpunctatus* (Hentz) (Araneae: Salticidae), which was

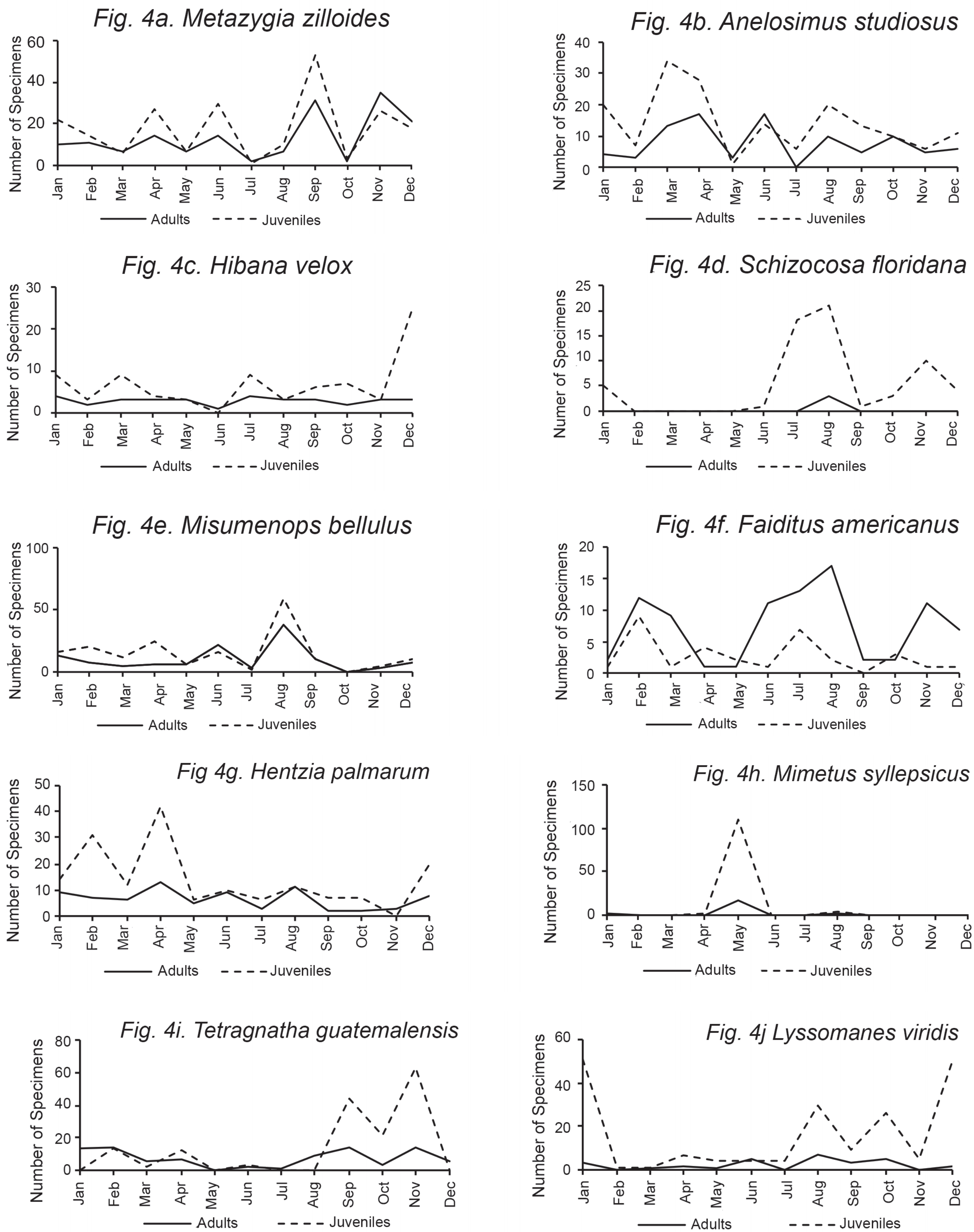

Fig. 4a-j. Seasonal life cycles of 10 abundant Everglades spider species.

found throughout the yr in the north but only during the winter in the Everglades samples. *Leucauge venusta* (Walckenaer) (Araneae: Tetragnathidae) and possibly *Colonus sylvanus* (Hentz) (Araneae: Salticidae) were present yr-round in the Everglades and in North Carolina. They have similar, nearly yr-round seasonal cycles in both locations. We include these data here only because it may encourage others to make a more extensive study of these phenomena.

Discussion

The characteristic 4 seasons of the continental US give way in south Florida to only 2 seasons: wet and dry, characterized by warm, humid, rainy summers, and mild, dry winters. The Everglades summer "wet" season extends from about mid-May to Nov, with temperatures ranging up to 30 to 35 °C, and an average annual rainfall of about 152 cm. The winter "dry" season extends from about Dec to mid-May, with temperatures ranging from 12 to 25 °C and low humidity (National Park Service 2015). Continental weather fronts occasionally bring near-freezing temperatures to south Florida.

That the environment plays a major role in determining what type of plant community develops in a given area is not questioned. Moreover, every major plant community is greatly influenced by 1 or more dominant plant species, and these dominants can change the environment of a region significantly, depending on the form and structure produced by the dominant species. Since the resulting plants produce additional changes by their mere presence, the environment itself is constantly changing as species are added or deleted. This investigation has shown that the spider species in the Everglades are associated characteristically with certain types of plant communities. Earlier work by Berry (1967), and others (Duffey 1962) showed that a spider tends to choose a plant form, not necessarily a plant species as its habitat. Species found in sawgrass were not found in hardwood hammocks, and vice versa. The overall form of the plant community may determine habitat choices. Probably the 2 most important components of the spider's environment are the physical factors of the habitat, and form or structure of the habitat. Early on, Peck (1967) attempted to compare the published results of 5 ecological investigations on spiders. From the great variation in species found in the different studies, he reasoned that perhaps temperature, humidity, and other ecological and ethological factors influence spider distribution more critically than had theretofore been recognized.

Perhaps our greatest surprise was that the percentage of Neotropical species was not higher than the 3% we found. With the Everglades being at the junction of the Nearctic and Neotropical ecozones, it would be reasonable to assume that the spider fauna would be a more balanced distribution of Nearctic and Neotropical species. Our data do not support this. Forty-six percent of the Everglades species appeared to be of Nearctic origin, 37% of Nearctic/Neotropical origin, and only 3% were of truly Neotropical origin (Table 1). Of the 201 identified species, a plurality (89 species) was from the Nearctic. The next largest group was a mixture of Nearctic and Neotropical (NA/NT). Seventy-six species were broadly distributed across the Nearctic and Neotropical regions with a fairly high concentration in the US and the Caribbean. Twenty-five species we consider to be Cosmopolitan; of these, 4 (Table 1) are considered to be non-natives based on both their distribution patterns and those of their close relatives, and have been moved widely by human agency. However, none of these (but see *Z. berryi* below) are restricted to Florida or the Everglades region. Our species list shows that only 2.5% of the Everglades fauna is introduced, a positive finding. The smallest number of species (8) was from the Neotropical region. Perhaps the not-infrequent cold spells that reach the Everglades prevent the more tropical species from becoming permanent residents. It would be worthwhile to make a comparison of the spiders in the Everglades versus those of Key West, Florida, USA, only 80 km further south, where freezing temperatures do not occur. Although temperatures below 0 °C occur in the Everglades, temperatures below 5 °C have never been recorded in Key West (National Weather Service 2019). Comparing these 2 regions can bring further insight into whether the preponderance of Nearctic species is due more to climatic or biogeographic factors (i.e., proximity to a large Nearctic landmass and lack of oceanic barrier).

Some specimens have been tentatively assigned to a genus (*Opopaea* and *Psilochorus*) but await more thorough examination by specialists for species placement. A number of species (*Modisimus* sp. and species denoted as "cf." in Table 1) are hypothesized to be undescribed. One species has been newly described as *Zodarion berryi* Bosmans and Draney (Araneae: Zodariidae) (Bosmans & Draney 2018). Given the distribution of other *Zodarion* species, it is highly likely that this species has been introduced to the park by human agency from the Old World. Although all known specimens of *Z. berryi* are from Everglades National Park, all specimens were found in a trash pile near the park entrance, and this habitat information supports the non-native hypothesis (Bosmans & Draney 2018).

There were 2 major categories of spider distribution. The "open" (without a woody canopy) sawgrass community tended to have 1 group of species, and the more "closed" communities (willow, pineland, and hammock) have other groupings, each different from the other. When the "closed" communities are compared to each other, the hammocks differ from willow and pineland communities. However, when the pineland community is compared to the sawgrass community, a very low level of similarity results.

Some spider species are associated with particular plants (e.g., sawgrass and the salticid *Marpissa pikei* (Peckham & Peckham) (Araneae: Salticidae). It is reasonable to conclude that it is the plant form (and associated environmental conditions) and not the plant species itself that determines the distribution of the spider. Spiders of the mangroves would be a useful addition to knowledge of the Everglades.

Many species were represented by so few specimens that it is impossible to make a prediction where their "center of distribution" might be. Forty-six species (22.9%) were represented in our collections by only 1 individual, and 81 species (40.3%) by 3 or fewer. They could be either relatively rare or else usually found in micro-niche habitats (rotten logs, streams, bromeliads, etc.).

Table 2. Common species found in each Everglades habitat, listed in descending abundance.

Sawgrass	Willowhead	Pinelands	Hammock
Tetragnatha pallescens	*Metazygia zilloides*	*Hentzia palmarum*	*Lyssomanes viridis*
Neoscona pratensis	*Anelosimus studiosus*	*Misumenops bellulus*	*Anelosimus studiosus*
Eris flava	*Pisaurina undulata*	*Mangora spiculata*	*Leucauge venusta*
Tetragnatha caudata	*Tetragnatha guatemalensis*	*Mangora gibberosa*	*Colonus sylvanus*
Pisaurina undulata	*Theridion flavonotatum*	*Zygoballus sexpunctatus*	*Leucauge argyra*
Hentzia grenada	*Neoscona arabesca*	*Meotipa pulcherrima*	*Mimetus syllepsicus*

Table 3. Sorensen Analysis of pinelands, hammock, willowhead, and sawgrass to determine overlaps in overall species compositions. "ab" represents shared species, "a" represents total species in the first habitat, and "b" represents total species in the second habitat.

Sorensen Analysis				(Percent similarity)
Habitat pairs:	ab	a	b	2(ab)/a+b
Pineland/hammock	51	86	133	0.4657
Pineland/sawgrass	14	86	44	0.2153
Pineland/willowhead	25	86	69	0.3225
Hammock/sawgrass	24	133	44	0.2711
Hammock/willow	28	133	69	0.2772
Sawgrass/willow	24	44	69	0.4247
Mean percent similarity				0.3294

We originally expected to describe the seasonal distribution of all 201 species, but it quickly became obvious that it was not possible. As mentioned above, some species pass through the cooler mo as adults, others as juveniles or eggs. Some species obviously are winter species, others are found only in the warm mo, and some are present yr-round. (Barnes 1953; Barnes & Barnes 1955). Generally, the population peak in the Everglades Nearctic species was about a mo or so before population peaks of Nearctic species from farther north (see Berry 1970 for North Carolina and Muma & Muma 1949 for Nebraska.)

Regardless of park management, global warming-related sea level rise is predicted to drastically change the nature of the Everglades National Park in the coming century (Overpeck & Weiss 2009). Records of organisms collected in this park (and their associated voucher specimens) from the mid-20th century and the early 21st century obviously can no longer be obtained, and their value to ecologists, conservationists, and perhaps even historians is likely to continue to increase over time.

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