

Analysis of body size, web size, and diet in two congeneric orb-weaving spiders (Araneae: Araneidae) syntopic in Florida scrub

James E. Carrel¹, and Mark Deyrup²

Abstract

The yellow garden spider, *Argiope aurantia* Lucas (Araneae: Araneidae), is widespread in North America, whereas the Florida garden spider, *Argiope florida* Chamberlin & Ivie (Araneae: Araneidae), is restricted to scrub habitats in the southeastern USA. Both orb-weavers occur syntopically in native oak scrub at the Archbold Biological Station in Highlands County, Florida. We hypothesized that female spiders of both species might have a high degree of dietary niche overlap because their orb-webs are located near each other, despite the fact that they may differ in body size and web characteristics. We located 180 side-by-side pairs of mature *A. aurantia* and *A. florida*, and assigned them at random into 3 treatment groups of 60 pairs each. *Argiope aurantia* in group 1 were more heavy-bodied and longer legged than *A. florida*. In group 2, the orb-webs of both species were hung at the same height aboveground, but *A. aurantia* webs were larger with fewer sticky spirals than those of *A. florida*. Over the course of 5 d, the 2 spider species in group 3 captured almost the same number of aerial arthropods (80 for *A. aurantia*; 76 for *A. florida*). We identified most prey (94%) to genus or species. Dietary niche overlap at the ordinal level was extensive (70%), but it shrank dramatically when calculated at the generic/species level (20%). We concluded that not only were *A. aurantia* consuming substantially larger prey than *A. florida*, but also that they were feeding on different kinds of aerial insects moving through gaps in oak scrub.

Key Words: predation; prey selection; niche breadth; Meloidae

Resumen

La araña amarilla de jardín, *Argiope aurantia* Lucas (Araneae: Araneidae), está muy extendida en América del Norte, mientras que la araña de jardín de la Florida, *Argiope florida* Chamberlin & Ivie (Araneae: Araneidae), está restringida a hábitats de matorral en el sureste de los Estados Unidos. Ambas son tejedoras de orbes (que hacen su telararaña en forma de una espiral) que ocurren sinópticamente en el matorral de roble nativo en la Estación Biológica Archbold en Condado de Highlands, Florida. Supusimos que las arañas hembras de ambas especies podrían tener un alto grado de superposición de nichos dietéticos debido a que sus telararañas-orbes están ubicadas cerca unas de otras, a pesar del hecho de que pueden diferir en el tamaño del cuerpo y las características de la red. Localizamos 180 pares de *A. aurantia* y *A. florida* maduros viviendo lado a lado y los asignamos al azar en 3 grupos de tratamiento de 60 pares cada uno. *Argiope aurantia* en el grupo 1 tenía un cuerpo más pesado y patas más largas que *A. florida*. En el grupo 2, las redes de orbe de ambas especies se colgaron a la misma altura sobre el suelo, pero las redes de *A. aurantia* fueran más grandes y con menos espirales pegajosas que las de *A. florida*. En el transcurso de 5 días, las 2 especies de arañas del grupo 3 capturaron casi la misma cantidad de artrópodos aéreos (80 para *A. aurantia*; 76 para *A. florida*). Identificamos la mayoría de las presas (94%) a nivel de género o especie. La superposición de nichos en la dieta a nivel ordinal fue extensa (70%), pero se redujo drásticamente cuando se calculó a nivel genérico/de especie (20%). Concluimos que no solo *A. aurantia* consumía presas sustancialmente más grandes que *A. florida*, sino que también se alimentaban de diferentes clases de insectos aéreos que se movían a través de brechas en los matorrales de roble.

Palabras Clave: depredación; selección de presas; amplitud de nicho; Meloidae

Spiders are among the dominant predators on earth (Wise 1993; Bond et al. 2014; Cushing 2017). Although they cannot fly, the ability of most species to disperse long distances by ballooning on the wind allows spiders to colonize all continents except Antarctica (Foelix 2011; Bond et al. 2014). The immense diversity of spiders both in species number (some 47,700 species in > 100 families are currently recognized) and in body size permits exploitation of a wide range of habitats and arthropod prey (Bradley 2013; Foelix 2011; World Spider Catalog 2018). A primary adaptation of spiders is their widespread use of webs for prey capture; the complex architectural geometry and astonishing material properties of silk extend the functional phenotype of these

predators by orders of magnitude (Venner & Casas 2005 and references therein; Zschokke et al. 2006; Blamires 2010).

Predation by orb-weaving spiders has received considerable scientific attention. Numerous field studies show that the majority of captured prey are small relative to the size of host spiders, plus the spectrum of insects and spiders taken from orb-webs is not a random sampling of the number and taxonomic diversity of aerial insects and spiders in the environment (Nentwig 1982, 1985, 1987; Venner & Casas 2005; Zschokke et al. 2006; Blamires 2010). A prime example of such research focuses on araneid spiders in the genus *Argiope* (Araneae: Araneidae). These spiders are convenient because they construct large,

¹University of Missouri-Columbia, Division of Biological Sciences, Columbia, Missouri 65211-7400, USA; E-mail: carrelj@missouri.edu (J. E. C.)

²Archbold Biological Station, Venus, Florida 33960, USA; E-mail: mdeyrup@archbold-station.org (M. D.)

*Corresponding author; E-mail: carrelj@missouri.edu

flat, long-lived orb-webs that are easily detected hanging vertically in old fields, grasslands, and shrubby habitats (Levi 1968; Enders 1973, 1976). They are diurnally active, and the prey they wrap in silk may be identified readily to taxonomic order in the field, or removed for further study (Horton & Wise 1983; Stowe 1986). For example, surveys of predation by mature female yellow garden spiders, *Argiope aurantia* Lucas (Araneae: Araneidae), at 6 temperate localities in the eastern US found that 4 orders of insects accounted for three-quarters of 1,430 prey: Hymenoptera (38.5%), Orthoptera (16.3%), Coleoptera (10.9%), and Lepidoptera (10.8%) (Uetz et al. 1978; Brown 1981; Howell & El-lender 1984; McReynolds & Polis 1987; Blackledge & Wenzel 1999).

At the subtropical Archbold Biological Station in Highlands County in south-central Florida, numerous *A. aurantia* often occur close to *Argiope florida* Chamberlin & Ivie (Araneae: Araneidae), the Florida garden spider (Carrel 2008). These colorful congeners are similar in size, phenology, and orb-web structure; however, their geographic distributions are vastly different: *A. aurantia* ranges widely across North America from southeast Canada south to Guatemala, whereas *A. florida* is highly restricted to relatively xeric sand scrub from eastern North Carolina to south Florida (Levi 1968, 2004; Justice et al. 2005.).

We hypothesized that, even though their orb-webs are located more or less at the same height side-by-side in oak scrub at Archbold, the 2 species might have significant differences in their trophic niches that reflect subtle differences in the size of mature females and their webs. Alternatively, knowing that competitive interactions usually are rare or nonexistent between these spiders (Wise 1993), the 2 *Argiope* species might show extensive prey niche overlap, *sensu* Pianka (1973).

Furthermore, we took advantage of the fact that a remarkably high proportion of the insect and spider fauna found at Archbold have been identified taxonomically over the course of decades of diligent work by many entomologists, and now are deposited in the Station's Collection of Arthropods. Hence, we were uniquely equipped to assess dietary niche overlap at 3 taxonomic levels (order, family, and genus/species), which to our knowledge has never been reported in a study of this kind.

Materials and Methods

STUDY AREA

The Archbold Biological Station is located 12 km south of the town of Lake Placid in Highlands County, Florida, near the southern terminus of the sandy Lake Wales Ridge (27.183333°N, 81.350000°W). The predominant vegetative associations in the study area, comprising 280 ha of the Station that is very flat (elevation 38–42 masl), are scrubby flatwoods, which are dominated by low (1–2 m high) shrubby oaks (*Quercus inopina* Ashe, *Quercus chapmanii* Sargent, *Quercus geminata* Small; all Fagaceae) and palmettos (*Serenoa repens* (Bartram) Small, and *Sabal etonia* Swingle ex Nash; both 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) Sarg.; Pinaceae), and an understory of xerophytic shrubs and flatwoods, with open stands of south Florida slash pine (*Pinus elliotii* var. *densa* Little & Dorman; Pinaceae) and an understory and ground cover of mesic grasses, herbs, saw palmetto (*S. repens*), and assorted shrubs (Abrahamson et al. 1984; Menges 1999; Deyrup & Deyrup 2012). The entire study area had regrown after it was consumed 5 yr earlier by a wildfire of unparalleled high intensity that produced a burn of unprecedented homogeneity at Archbold; all shrubs and forbs had been burned to ground level (Abrahamson & Abrahamson 2002).

In Sep 2006, both orb-weavers were numerous (60–80 newly matured females of each per ha) across most of Archbold. We located 180 pairs of *A. aurantia* and *A. florida* females whose orb webs were only 5 to 10 m apart. Each pair was assigned at random to 1 of 3 treatment groups: spider body size, orb-web characteristics, or prey determination. No spiders were harmed in this study.

SIZE OF ARGIOPE SPP.

We used 2 body size measures as indicators of foraging success in *A. aurantia* and *A. florida* females. Spider wet weight is known to reflect lifetime foraging success, whereas length of the first leg reflects foraging success prior to the final molt (Herberstein & Heiling 1998 and references therein).

We carefully removed 60 spiders of both *Argiope* species from their webs and took them to the laboratory where they were anesthetized with carbon dioxide gas and weighed to the nearest 0.1 mg on an electronic balance. Subsequently, the length of the first right leg (tarsus to coxa) was measured to the nearest 0.1 mm using a caliper (Model 144MM, General Tools and Instruments, Secaucus, New Jersey, USA). All 120 spiders were returned to their webs. Interspecific differences in mean body sizes were evaluated using Student's t-test (GraphPad QuickCalcs 2017).

ORB-WEBS OF ARGIOPE SPECIES

We used the method of Herberstein and Tso (2000) to characterize the size and shape of 60 orb-webs of each *Argiope* species in the field. Using a metallic tape measure, we determined the height to the center of the hub of the orb-web above ground (h), the horizontal diameter of the orb-web (d_o), the length of the upper vertical radius (r_u), the length of the lower vertical radius (r_l), the length of the upper hub radius (Hr_u), and the length of the lower hub radius (Hr_l) to the nearest mm. We then counted the number of sticky spiral threads in the upper and lower halves of the web (S_u and S_l , respectively). Using the formulas presented by Herberstein and Tso (2000), we calculated the capture area (in cm^2) and the mesh height, and the average distance between adjacent sticky spiral threads (in mm), for each web. Interspecific differences in mean web measurements were evaluated using Student's t-test (GraphPad QuickCalcs 2017).

PREY OF ARGIOPE SPECIES

We marked the location of 60 pairs of webs occupied by *A. aurantia* and *A. florida* females in the native scrub with stake flags so that we could quickly find them at dawn and dusk. Initially, we removed all prey hanging in each web in late afternoon, then we returned the next d after dawn (7:00 AM to 9:00 AM) and before dusk (5:00 PM to 7:00 PM) for 5 consecutive d, and carefully removed with forceps all arthropods trapped in a web or being eaten by the resident spider. 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 (Model SZX12, Olympus Corporation, Shinjuku, Tokyo, Japan). 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 and consumable dry body mass to the nearest 0.1 mg using taxa-specific regression equations (Sample et al. 1993; Sabo et al. 2002; Straus & Aviles 2018). Differences in captured prey at

the ordinal level were evaluated statistically using the Chi square test (GraphPad QuickCalcs 2017).

We determined the trophic niches of the 2 spiders using the Schoener overlap index, one of the simplest and most attractive measures of niche overlap (Krebs 1989). This index measures the percentage similarity of prey between 2 species, the actual area of overlap of their resource utilization curves. We did this at 3 taxonomic levels: order, family, and species.

Results

SIZE OF *ARGIOPE* SPIDERS AND THEIR ORB-WEBS

Argiope aurantia females were consistently larger than *A. florida* females according to the 2 measurements we made. As shown in Table 1, living *A. aurantia* females were typically 2.2 times heavier than *A. florida* females. In addition, the first right legs of *A. aurantia* averaged 1.3 times longer than those of *A. florida*.

Both spiders hung their webs in the scrubby vegetation at essentially the same height aboveground (ca. 1.1 m on average to the hub). But according to the other 7 measures (Table 1), the 2 species produced significantly different orb-webs.

Orb-webs of *A. aurantia* on average were 1.3 to 1.5 times wider on the horizontal and vertical axes than *A. florida* orb-webs, and the calculated difference in prey capture area was even greater (1.9 times in favor of *A. aurantia*).

On average, there were 50 and 65 sticky spirals in the upper and lower halves of *A. florida* orb-webs, which was 1.5 times more than those in a typical *A. aurantia* web (34 and 42, respectively). This meant that the average mesh height in *A. aurantia* (5.1 mm) was 2.2 times greater than that in *A. florida* orb-webs (2.3 mm). Our findings mirror those of Uetz et al. (1978), who reported mean mesh heights of 4.6 mm and 2.7 mm for *A. aurantia* and *A. trifasciata* (Forskål), the banded garden spider, respectively, sympatric in an Illinois prairie.

PREY OF *ARGIOPE* SPIDERS

Over the course of 5 d we collected about the same number of arthropods from the 2 species: 80 items for *A. aurantia* and 76 for *A. florida*. We removed two-thirds more prey from spiders late in the d than at dawn, strongly suggesting that both species were primarily diurnal hunters. There was no statistically significant difference between

the 2 species in number of prey captured at dawn versus dusk ($\chi^2 = 0.194$; $df = 1$; $P = 0.66$).

Prey trapped by *A. aurantia* were substantially larger than that of *A. florida* (Table 1). On average, insects in *A. aurantia* webs were 1.6 times longer and 2.4 times heavier than those in *A. florida* webs.

We were able to identify taxonomically 94% (= 146 of 156) of the specimens to genus or species, respectively (Table 2). Inspection of the prey list revealed some interesting differences between the spiders. Small homopterans were entirely absent from webs of *A. aurantia*, whereas spiders and neuropterans were missing from *A. florida* webs. Large robber flies (Asilidae), dragonflies (Aeshnidae and Libellulidae), and leather-colored bird grasshoppers (*Schistocerca alutacea* Harris; Orthoptera: Acrididae) were present only in *A. aurantia* webs, but medium-size blister beetles (Meloidea) and horseflies (Tabanidae) were retrieved only from *A. florida* webs.

Of the 15 insects found in both spiders' webs, half were orthopterans. Six species were represented by more than singletons: acorn weevils (*Cucurlio* sp.; Curculionidae), female fire ants (*Solenopsis invicta* Buren; Hymenoptera: Formicidae), southern yellowjackets (*Vespula squamosa* (Drury); Hymenoptera: Vespidae), toothcercus shortwing grasshoppers (*Melanoplus forcipatus* Hubbell; Orthoptera: Acrididae), spotted-winged grasshoppers (*Orphulella pelidna* (Burmeister); Orthoptera: Acrididae), and glassy-winged toothpick grasshoppers (*Stenacris vitreipennis* (Marschall); Orthoptera: Acrididae).

Insects known to be endemic to Florida scrub were exceedingly uncommon in the diets of both spider species. Only 6 specimens (4% of all prey) belonging to 3 species were collected: 1 elongate June beetle (*Phyllophaga elongata* (Linell); Coleoptera: Melolonthidae) in an *A. florida* web; 1 nigropicta grasshopper (*Aptenopedes nigropicta* Hebard; Orthoptera: Acrididae) each in *A. aurantia* and *A. florida* webs; and 2 and 1 toothcercus shortwing grasshoppers (*M. forcipatus*), respectively, in *A. aurantia* and *A. florida* webs. These results are the opposite of our initial hypothesis that *A. florida*, being found mostly in xeric, scrubby habitats in the southeastern United States, may tend to prefer scrub-adapted insects in their diet.

DIETARY NICHE ANALYSES FOR *ARGIOPE* SPIDERS

As shown in Table 3, the taxonomic diversity of prey of the 2 *Argiope* species was very similar. There was not a significant interspecific difference in the number of prey captured at the ordinal level ($\chi^2 = 9.39$; $df = 5$; $P = 0.0946$). However, there was a highly significant differ-

Table 1. Comparison of spider sizes, orb-webs, and prey parameters for 2 *Argiope* species ($N = 60$ females per group). Values for each spider species represent the mean \pm SD.

Group	Parameter	Parameter	<i>A. florida</i>	Student's <i>t</i>	<i>P</i>
Spider	Body wet mass (mg)	845.0 \pm 367.0	377.0 \pm 115.0	9.43	< 0.001
	Body length (mm)	22.4 \pm 2.8	15.7 \pm 1.5	16.38	< 0.001
	Leg length (mm)	36.6 \pm 3.1	28.2 \pm 3.2	14.60	< 0.001
Orb-web	Hub height (cm)	104.5 \pm 25.0	111.5 \pm 19.5	1.71	0.0899
	Horizontal diam (cm)	48.9 \pm 10.1	37.4 \pm 6.2	7.52	< 0.001
	Upper vertical radius (cm)	23.5 \pm 5.9	15.6 \pm 3.6	8.85	< 0.001
	Lower vertical radius (cm)	30.2 \pm 6.4	20.8 \pm 3.7	9.85	< 0.001
	Sticky spirals upper web half (no.)	34.0 \pm 8.7	50.5 \pm 13.6	7.92	< 0.001
	Sticky spirals lower web half (no.)	42.5 \pm 9.0	64.7 \pm 14.1	10.28	< 0.001
	Capture area (cm ²)	1930.0 \pm 760.0	1010.0 \pm 300.0	8.72	< 0.001
	Mesh height (mm)	5.1 \pm 1.4	2.3 \pm 0.6	14.24	< 0.001
	Prey	Body length (mm)	18.1 \pm 10.5	11.4 \pm 7.2	4.62
Body dry mass (mg)		73.7 \pm 85.6	30.9 \pm 40.4	3.96	< 0.001
Body consumable dry mass (mg)		35.7 \pm 43.8	16.9 \pm 21.8	3.40	0.001

Table 2. Prey of 60 female *Argiope aurantia* and 60 *Argiope florida*.

Order	Family	Species	<i>A. aurantia</i>	<i>A. florida</i>
Araneae	Lycosidae	<i>Hogna ceratiola</i> Gertsch & Wallace	1	0
Coleoptera	Buprestidae	<i>Chrysobothris</i> sp.	1	0
		<i>Chauliognathus marginalis</i> Casey	0	1
	Cantharidae	<i>Zagymnus clerinus</i> (LeConte)	2	0
		<i>Enaphalodes hispicornis</i> (L.)	1	0
	Chrysomelidae	<i>Disonycha caroliniana</i> (F.)	0	1
		<i>Exema</i> sp.	1	0
		<i>Rhabdopterus angustipennis</i> Schultz	1	0
		<i>Curculio</i> sp.	4	3
	Curculionidae	<i>Odontocorynus</i> sp.	1	0
		<i>Polydrusus</i> sp.	1	0
		unknown	1	0
	Elateridae	unknown	1	0
	Meloidae	<i>Epicauta batesii</i> Horn	0	2
		<i>Epicauta heterodera</i> Horn	0	6
	Scarabaeidae	<i>Ataenius</i> sp.	0	1
		<i>Boreocanthon depressipennis</i> (LeConte)	1	1
		<i>Diploptaxis bidentata</i> LeConte	0	2
		<i>Melanocanthon punctaticollis</i> (Schaeffer)	0	4
		<i>Onthophagus hecate blatchleyi</i> Brown	1	1
		<i>Onthophagus tuberculifrons</i> Harold	0	3
<i>Phyllophaga dispar</i> (Burmeister)		1	0	
<i>Phyllophaga elongata</i> (Linell)		0	1	
<i>Trigonopeltastes delta</i> (Forster)		2	0	
<i>Hymenorus</i> sp.		0	1	
Diptera	Asilidae	<i>Diogmites</i> sp.	5	0
	Tabanidae	<i>Tabanus</i> sp.	0	2
	Tipulidae	Unknown	0	1
Heteroptera	Coreidae	<i>Acanthocephala confraterna</i> (Uhler)	1	0
		<i>Leptoglossus phyllopus</i> (L.)	1	0
	Pentatomidae	<i>Euschistus</i> sp.	1	1
		<i>Oebalus pugnax</i> (F.)	0	1
	Reduviidae	<i>Zelus longipes</i> L.	1	0
	Scutelleridae	<i>Diolcus chrysorrhoeus</i> (F.)	0	1
Unknown	Unknown	1	0	
Homoptera	Cercopidae	<i>Prosapia bicincta</i> (F.)	0	1
	Cicadellidae	<i>Jikradia melanota</i> (Spångberg)	0	2
		<i>Paraphlepsius</i> sp.	0	1
	Membracidae	<i>Spissitilus festinus</i> (Say)	0	1
Hymenoptera	Apidae	<i>Apis mellifera</i> L.	0	1
		<i>Bombus impatiens</i> Cresson	1	0
	Bethylidae	<i>Pristocera</i> sp.	0	1
	Formicidae	<i>Brachymyrmex depilis</i> Emery	0	2
		<i>Brachymyrmex obscurior</i> Forel	0	2
		<i>Pseudomyrmex gracilis</i> (F.)	1	1
		<i>Solenopsis invicta</i> Buren	1	4
		<i>Agapostemon splendens</i> Lepeletier	1	0
	Halictidae	<i>Augochlora aurata</i> (Smith)	0	2
		<i>Augochlora pura</i> Say	1	0
		<i>Augochloropsis sumptuosa</i> (Smith)	0	1
		<i>Megachile brevis pseudobrevis</i> Mitchell	0	1
	Mutillidae	<i>Dasymutilla asopus bexar</i> (Blake)	1	1
		<i>Dasymutilla nigripes</i> (F.)	0	1
	Sphecidae	<i>Isodontia exornata</i> Fernald	1	0
		<i>Liris</i> sp.	0	1
	Vespidae	<i>Vespula squamosa</i> (Drury)	9	5
		<i>Polistes dorsalis</i> (F.)	1	0
	Lepidoptera	Noctuidae	Unknown	3

Table 2. (Continued) Prey of 60 female *Argiope aurantia* and 60 *Argiope florida*.

Order	Family	Species	<i>A. aurantia</i>	<i>A. florida</i>	
Neuroptera	Chrysopidae	Unknown	1	0	
	Mymeleontidae	<i>Vella americana</i> (Drury)	1	0	
Odonata	Aeshnidae	<i>Anax junius</i> (Drury)	1	0	
	Libellulidae	<i>Celithemis bertha</i> Williamson	0	1	
		<i>Erythrodiplax minuscula</i> (Rambur)	3	0	
		<i>Pachydiplax longipennis</i> (Bermeister)	2	0	
		<i>Tramea carolina</i> (L.)	0	1	
Orthoptera	Acrididae	<i>Aptenopedes nigropicta</i> Hebard	1	1	
		<i>Aptenopedes sphenaroides</i> Scudder	1	1	
		<i>Aptenopedes</i> sp.	3	0	
		<i>Dichromorpha elegans</i> (Morse)	1	1	
		<i>Melanoplus forcipatus</i> Hubbell	2	1	
		<i>Orphulella pelidna</i> (Burmeister)	1	2	
		<i>Schistocerca alutacea</i> (Harris)	9	0	
		<i>Spharagemon marmota picta</i> (Scudder)	0	2	
		<i>Stenacris vitreipennis</i> Marschall	2	2	
		Unknown	1	0	
	Gryllidae	<i>Hapithus agitator</i> (Uhler)	1	0	
	Tetrigidae	<i>Tettigidea lateralis</i> (Say)	1	1	
	total			80	76

ence between the spiders when consumable dry biomass was estimated ($\chi^2 = 189.33$; $df = 5$; $P < 0.001$). Two orders of insects set them apart; *A. aurantia* obtained more biomass from dipterans and less from coleopterans than expected by chance, whereas the opposite held true for *A. florida*, where adult females ate more coleopterans and fewer dipterans than expected by chance.

Table 3. Contrast between taxonomic composition of prey captured by adult female *Argiope* spiders ($N = 60$ each). Other taxa include Araneae, Hemiptera, Lepidoptera, and Neuroptera. The table provides the following information: observed cell totals, (expected cell totals), and [Chi-square statistic for each cell].

Order	Number of individuals captured	
	<i>A. aurantia</i>	<i>A. florida</i>
Coleoptera	18 (23.08) [1.12]	27 (21.92) [1.18]
Diptera	5 (4.10) [0.20]	3 (3.90) [0.21]
Hymenoptera	17 (20.51) [0.60]	23 (19.49) [0.63]
Odonata	6 (4.10) [0.88]	2 (3.90) [0.92]
Orthoptera	23 (17.44) [1.78]	11 (16.56) [1.87]
5 other taxa	11 (10.77) [0.00]	10 (10.23) [0.01]
Total	80	76

$\chi^2 = 9.39$; $df = 5$; $P = 0.0946$

Order	Consumable dry mass of individuals captured (mg)	
	<i>A. aurantia</i>	<i>A. florida</i>
Coleoptera	305 (417.80) [30.45]	272 (159.20) [79.92]
Diptera	359 (289.63) [23.50]	41 (110.37) [43.60]
Hymenoptera	447 (461.24) [0.44]	190 (175.76) [1.15]
Odonata	422 (440.97) [0.82]	187 (168.03) [2.14]
Orthoptera	1459 (1401.10) [2.39]	476 (533.90) [6.28]
5 other taxa	249 (230.26) [1.53]	69 (87.74) [4.00]
Total	3,241	1,235

$\chi^2 = 189.33$; $df = 5$; $P < 0.001$

Because we were able to identify almost all prey items to genus or species, we calculated the dietary overlap of the 2 spiders at 3 taxonomic levels using Schoener's similarity index. The dietary niche overlap dwindled from 70% of 10 orders shared, down to 39% of 36 families held in common, all the way to 20% of 76 genera or species found at least once in orb-webs of both species (Table 4). Thus, taxonomic scale mattered greatly; what seemed to be a high degree of commonality with a coarse niche filter was completely reversed when a much finer filter was applied. We conclude there was little overlap in the kinds of prey eaten by the spiders, even though they were trapping aerially active arthropods side-by-side in what appeared to be the same scrubby habitat.

Discussion

The sizes of *Argiope* used in our study and their orb-webs (Table 1) were very similar to values reported by other authors. Mean body lengths of *A. aurantia* and *A. florida* presented were almost identical to values published by Elgar (1991), McReynolds and Polis (1987), and Blackledge (2011). The average diameter of *A. aurantia* orb-webs we measured in the Florida scrub was 3 to 8 cm wider than webs of this species in Tennessee and Mississippi (McReynolds and Polis 1987; McReynolds 2000). Comparable data for *A. florida* were not available. The orb-webs of both *Argiope* were quite high in the scrub; the hubs typically were slightly more than a m aboveground. The reason for this is that spiders in most instances suspended their webs from 1.5 to 2 m tall woody vegetation, placing the orbs across flight paths of scrub insects (Justice et al. 2005; Carrel & Deyrup 2014). Other studies report hub-heights for *A. aurantia* averaging 64 to 66 cm, about two-thirds of our findings (Enders 1974; McReynolds & Polis 1987; McReynolds 2000). The lower elevations in these studies almost certainly is because they were performed in old fields and other north temperate habitats dominated by relatively low growing grasses and herbaceous vegetation.

Table 4. Dietary niche overlap in 2 *Argiope* species at 3 taxonomic levels.

Taxa	Prey richness (number of taxa)			
	Either <i>A. species</i>	<i>A. aurantia</i> only	<i>A. florida</i> only	Niche overlap: both <i>A. spp.</i> in common (% of total)
Orders	10	9	8	7 (70%)
Families	36	25	25	14 (39%)
Genus or species	76	46	46	15 (20%)

Despite having an orb-web with almost twice the capture area (Table 1), *A. aurantia* captured almost the same number of aerial prey as *A. florida*. Perhaps *A. aurantia* webs are less efficient per unit capture area than those of *A. florida*, because webs of the former have only two-thirds as many sticky spirals on average, and the gaps between sticky silken threads are more than twice as great as the latter species (Table 1). Small (4–6 mm long) beetles and wasps that got caught in *A. florida* webs likely would fly through *A. aurantia* orbs unharmed. Unfortunately, the relationship between design of webs and prey capture is complex and unclear. A review of data for 17 species of orb-weavers showed there is no significant correlation between mean mesh height and mean length of prey captured (Herberstein & Heiling 1998). Incidentally, the rate of prey capture by both *Argiope* females (about 1 item per spider every 4 d) was identical to the rate we reported previously for mature red widow spiders, *Latrodectus bishopi* Kaston (Araneae: Theridiidae), in late winter before the palmettos begin to flower in the scrub at Archbold (Carrel & Deyrup 2014).

Most prey (72% by count) caught by *A. aurantia* females in our study belonged to 3 insect orders (Orthoptera > Coleoptera > Hymenoptera [Table 3]), which was quite different than the ordinal ranking reported for this species' prey in the 5 studies mentioned in the introduction (Hymenoptera > Orthoptera > Coleoptera = Lepidoptera). We suspect this difference is explained by the striking contrast in the abundance of flowering plants at the study sites. Florida scrub in Sep is largely lacking in flowering herbs and shrubs; inflorescences of *Palafoxia feayi* Gray (Asteraceae), a lanky endemic perennial, and few others are scattered across the landscape. This contrasts dramatically with the northern temperate sites used by other authors: old fields, grasslands, and roadsides used by them were replete with verdant stands of goldenrods, asters, and many blooming herbs, such as smartweed, *Polygonum punctatum* Elliott (Polygonaceae), all of which are very attractive to bees and wasps. If one discounts the hymenopterans, then the rankings of their studies and ours become similar: orthopterans and coleopterans are top-ranked prey of *Argiope*.

We extracted 8 silk-encased blister beetles, *Epicauta* spp. Dejean (Coleoptera: Meloidae), from webs of *A. florida* but none from *A. aurantia*. These field-derived data validate the findings of Smedley et al. (1995) that *A. florida* readily feeds on living blister beetles flipped into their webs by experimenters, whereas almost all other spiders either ignore or reject meloids unharmed after an attack. Extensive field observations of more than 5,000 webs made over the past 12 yr at Archbold add additional support; we recorded 15 instances of *Epicauta* spp. being eaten by mature Florida garden spiders, but none by yellow garden spiders (J. Carrel, unpublished observations).

Orthopterans, particularly short-horned grasshoppers (Acrididae), were the most important taxon in the diets of both *Argiope*. They were common in the spiders' prey base (comprising 28% and 14% of all items captured by *A. aurantia* and *A. florida*, respectively) (Table 3). Furthermore, they contributed 45% and 39% of the estimated biomass consumed by female *A. aurantia* and *A. florida*, far more than any other insect order (Table 3). Odonates, although uncommon in the prey base, because their large size contributed disproportionately to

the consumable biomass of both spiders (13% and 15% for *A. aurantia* and *A. florida*, respectively).

The "rare, large prey" hypothesis espoused by Blackledge (2011) argues that orb-weavers in general derive the bulk of their energy from a small subset of the largest possible insects flying in their habitats. He supported his argument by compiling a meta-analysis of published data on the diets of 31 species of orb-weavers. He defined large prey as "insects at least 66% as long as the spiders capturing them." When applied to our data, we found that 64% and 41% of prey items of *A. aurantia* and *A. florida*, respectively, were large insects; they comprised 92% and 79% of the respective spider's consumable biomass. Hence, we reject the rare, large prey hypothesis for *Argiope* living in subtropical Florida scrub.

Dietary niches of spiders have been documented mainly for species feeding in agroecosystems to evaluate their potential as biological control agents. Nyffler (1999) reviewed 40 published studies of 5 families of orb-weavers and 4 families of hunters performed in Europe and the US. He found 10 insect orders and Araneae make up the bulk of prey of these spiders, regardless of hunting mode. As noted by Wise (1993), pair-wise studies of types of prey used by sympatric spiders are uncommon. Horton and Wise (1983) were among the first to document wide overlap in types of prey used by the orb-weavers *A. aurantia* and *A. trifasciata*. They calculated the Schoener overlap index for number of prey in each order to be considerable (≥ 0.69) over the course of 2 yr. McReynolds & Polis (1987) subsequently obtained similar results with these 2 orb-weavers. Nentwig (1985) also reported extensive niche overlap, Schoener index 0.8 to 0.9, for prey captured by 4 tropical orb-weavers. Recently, Wirta et al. (2015), using DNA barcode technology, identified 21 lepidopteran and 117 dipteran prey in the gut contents of a lycosid and 2 thomisid spiders living sympatrically in the depauperate high tundra of northeastern Greenland. They found all 3 spider species were wide generalists, overlap in prey use was high (Schoener index 0.58–0.63), and the results remained qualitatively unchanged regardless of whether prey identity was considered at the level of species, genus, or family. Perhaps if they had examined the entire insect and spider fauna, which they note consists of an additional ≥ 90 species of insects and spiders, then their results might be more taxon sensitive. By identifying almost all the prey captured by *A. aurantia* and *A. florida*, we confirmed that niche overlap is very sensitive to taxonomic scale; what appeared to be extensive overlap at the ordinal level, as reported by others, with pairs of *Argiope* species, dwindle to almost no overlap at the species level. Thus, these 2 spiders living syntopically in Florida scrub are consuming prey, not only of different sizes, but of different species. They are generalist predators in a diverse universe of prey species, none of which is especially likely to be captured by the spiders.

Acknowledgments

We thank the Archbold Biological Station for providing research facilities. Funding for this work came in part from the Development Fund at the University of Missouri-Columbia and the Archbold Biological Station.

References Cited

- Abrahamson WG, Abrahamson CR. 2002. Persistent palmettos: effects of the 2000–2001 drought on *Serenoa repens* and *Sabal etonia*. *Florida Scientist* 65: 281–292.
- Abrahamson WG, Johnson AF, Layne JN, Peroni PA. 1984. Vegetation of the Archbold Biological Station, Florida: an example of the southern Lake Wales Ridge. *Florida Scientist* 47: 209–250.
- Blamires SJ. 2010. Plasticity in extended phenotypes: orb web architectural responses to variations in prey parameters. *Journal of Experimental Biology* 213: 3207–3212.
- Blackledge TA. 2011. Prey capture in orb weaving spiders: are we using the right metric? *Journal of Arachnology* 39: 205–210.
- Blackledge TA, Wenzel JW. 1999. Do stabilimenta in orb webs attract prey or defend spiders? *Behavioral Ecology* 10: 372–376.
- Bond JE, Garrison NL, Hamilton CA, Godwin RL, Hedin M, Agnarsson I. 2014. Phylogenomics resolves a spider backbone phylogeny and rejects a prevailing paradigm for orb web evolution. *Current Biology* 24: 1765–1771.
- Bradley RA. 2013. *Common Spiders of North America*. University of California Press, Berkeley, California, USA.
- Brown KM. 1981. Foraging ecology and niche partitioning in orb-weaving spiders. *Oecologia* 50: 380–385.
- Carrel JE. 2008. The effect of season of fire on density of female garden orbweavers (Araneae: Araneidae: *Argiope*) in Florida scrub. *Florida Entomologist* 91: 332–334.
- Carrel JE, Deyrup M. 2014. Red widow spiders (Araneae: Theridiidae) prey extensively on scarab beetles endemic in Florida scrub. *Florida Entomologist* 97: 130–137.
- Cushing PE. 2017. Introduction, pp. 1–16 *In* Ubick D, Paquin P, Cushing PE, Roth V [eds.], *Spiders of North America: An Identification Manual*, second edition. American Arachnological Society, Keene, New Hampshire, USA.
- Deyrup M, Deyrup L. 2012. The diversity of insects visiting flowers of saw palmetto (*Arecaceae*). *Florida Entomologist* 95: 711–730.
- Elgar MA. 1991. Sexual cannibalism, size dimorphism, and courtship behavior in orb-weaving spiders. *Evolution* 45: 444–448.
- Enders F. 1973. Selection of habitat by the spider *Argiope aurantia* Lucas (Araneidae). *American Midland Naturalist* 90: 47–55.
- Enders F. 1974. Vertical stratification in orb-web spiders (Araneidae, Araneae) and a consideration of other methods of coexistence. *Ecology* 55: 317–328.
- Enders F. 1976. Effects of prey capture, web destruction and habitat physiognomy on web-site tenacity of *Argiope* spiders (Araneidae). *Journal of Arachnology* 3: 75–82.
- Foelix RF. 2011. *Biology of Spiders*, third edition. Oxford University Press, New York, New York, USA.
- GraphPad QuickCalcs. 2017. GraphPad Software, La Jolla, California, USA. (online) <http://www.graphpad.com/quickcalcs/ConflInterval1.cfm> (last accessed 28 Feb 2019).
- Herberstein ME, Heiling AM. 1998. Does mesh height influence prey length in orb-web spiders (Araneae)? *European Journal of Entomology* 95: 367–371.
- Herberstein ME, Tso I-M. 2000. Evaluation of formulae to estimate the capture area and mesh height of orb webs (Araneidae, Araneae). *Journal of Arachnology* 28: 180–184.
- Horton CC, Wise DH. 1983. The experimental analysis of competition between two syntopic species of orb-web spiders (Araneae: Araneidae). *Ecology* 64: 929–944.
- Howell FG, Ellender RD. 1984. Observations on growth and diet of *Argiope aurantia* Lucas (Araneidae) in a successional habitat. *Journal of Arachnology* 12: 29–36.
- Justice MJ, Justice TC, Vesci RL. 2005. Web orientation, stabilimentum structure and predatory behavior of *Argiope florida* Chamberlin & Ivie 1944 (Araneae, Araneidae, Argiopinae). *Journal of Arachnology* 33: 82–92.
- Krebs CJ. 1989. *Ecological Methodology*. Harper & Row, New York, New York, USA.
- Levi HW. 1968. The spider genera *Gea* and *Argiope* in America (Araneae: Araneidae). *Bulletin of the Museum of Comparative Zoology* 136: 319–352.
- Levi HW. 2004. Comments and new records for the American genera *Gea* and *Argiope* with the description of a new species (Araneae: Araneidae). *Bulletin of the Museum of Comparative Zoology* 158: 47–66.
- McReynolds CN. 2000. The impact of habitat features on web features and prey capture of *Argiope aurantia* (Araneae, Araneidae). *Journal of Arachnology* 28: 169–179.
- McReynolds CN, Polis GA. 1987. Ecomorphological factors influencing prey use by two sympatric species of orb-web spiders, *Argiope aurantia* and *Argiope trifasciata* (Araneidae). *Journal of Arachnology* 15: 371–383.
- Menges ES. 1999. Ecology and conservation of Florida scrub, pp. 7–22 *In* Anderson RC, Fralish JS, Baskin JM [eds.], *Savannas, Barrens, and Rock Outcrop Plant Communities of North America*. Cambridge University Press, Cambridge, United Kingdom.
- Nentwig W. 1982. Why do only certain insects escape from a spider's web? *Oecologia* 53: 412–417.
- Nentwig W. 1985. Prey analysis of four species of tropical orb-weaving spiders (Araneae: Araneidae) and a comparison with araneids of the temperate zone. *Oecologia* 66: 580–594.
- Nentwig W. 1987. Prey of spiders, pp. 249–263 *In* Nentwig W [ed.], *Ecophysiology of Spiders*. Springer-Verlag, Berlin, Germany.
- Nyffler M. 1999. Prey selection of spiders in the field. *Journal of Arachnology* 27: 317–324.
- Pianka ER. 1973. The structure of lizard communities. *Annual Review of Ecology and Systematics* 4: 53–74.
- Sabo JL, Bastow JL, Power ME. 2002. Length-mass relationships for adult aquatic and terrestrial invertebrates in a California watershed. *Journal of the North American Benthological Society* 21: 336–343.
- Sample BE, Cooper RJ, Greer RD, Whitmore RC. 1993. Estimation of insect biomass by length and width. *American Midland Naturalist* 129: 234–240.
- Smedley SR, Blankespoor CL, Yuang Y, Carrel JE, Eisner T. 1995. Predatory responses of spiders to blister beetles (family Meloidae). *Zoology* 99: 211–217.
- Stowe M. 1986. Prey specialization in the Araneidae, pp. 101–131 *In* Shear WA [ed.], *Spiders: Webs, Behavior, and Evolution*. Stanford University Press, Stanford, California, USA.
- Straus S, Avilés L. 2018. Estimating consumable biomass from body length and order in insects and spiders. *Ecological Entomology* 43: 69–75.
- Uetz GW, Johnson AD, Schemske DW. 1978. Web placement, web structure, and prey capture in orb-weaving spiders. *Bulletin of the British Arachnological Society* 4: 141–148.
- Venner S, Casas J. 2005. Spider webs designed for rare but life-saving catches. *Proceedings of the Royal Society B* 272: 1587–1592.
- Wirta HK, Weingartner E, Hambaek PA, Roslin T. 2015. Extensive niche overlap among the dominant arthropod predators of the High Arctic. *Basic and Applied Ecology* 16: 86–92.
- Wise DH. 1993. *Spiders in Ecological Webs*. Cambridge University Press, Cambridge, United Kingdom.
- World Spider Catalog. 2018. World Spider Catalog. Version 19.5. Natural History Museum Bern, Switzerland. (online) <http://wsc.nmbe.ch> (last accessed 28 Feb 2019).
- Zschokke S, Hénaut Y, Benjamin SP, Garcia-Ballinas JA. 2006. Prey-capture strategies in sympatric web-building spiders. *Canadian Journal of Zoology* 84: 964–973.