Prey Selection and Predatory Importance of Orb-Weaving Spiders (Araneae: Araneidae, Uloboridae) in Texas Cotton

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ABSTRACT In an unsprayed cotton field in east Texas, orb weavers were one of the numerically dominant groups of spiders, constituting 10% of all spiders collected by D-vac during the summer of 1985 (range, 0.04 individuals/m² in June to 0.72 individuals/m² in August). Direct counts, conducted during peak orb-weaver density in August, showed that 0.86 individuals/m² were found. More than two-thirds of all orb weavers collected by D-vac in cotton consisted of the five species Acanthepeira stellata (Walckenaer), Neoscona arabesca (Walckenaer), Gea heptagon (Hentz), Tetragnatha laboriosa Hentz, and Uloborus glomosus (Walckenaer). Their prey consisted of insects (>99%) and spiders (<1%). Aphids, which occasionally reach pest status in Texas cotton, were the most abundant prey of all five spiders (34.6-90%). Other important prey included small dipterans, cicadellids, and hymenopterans. Furthermore, coleopterans were an important component in the prey of A. stellata and N. arabesca. Together, these five insect groups made up >90% of the prey of the orbweaving spiders, which are characterized as generalist predators. Differences among the five spider species indicate that prey selection was occurring; this seems to be determined by web location, web inclination, and web strength. Of the orb weavers occurring in cotton, 99% were small-sized spiders (primarily G. heptagon) that intercept small prey with their delicate (about 4 cm diameter) webs. These orb weavers are predators primarily of smallsized pests such as the cotton aphid, Aphis gossypii Glover, and the cotton fleahopper, Pseudatomoscelis seriatus (Reuter).

KEY WORDS Arachnida, orb-weaving spiders, cotton, predation

MOST SPECIES of Araneidae and Uloboridae spin spiraling orb webs. Although the general biology of orb-weaving spiders is well known (reviews in Witt et al. 1968, Levi 1978), the significance of these predators in the natural control of pest insects is poorly understood, although in some agroecosystems, orb weavers constitute the most abundant spiders. Prey analyses have been conducted in soybean fields in Illinois (LeSar & Unzicker 1978) and Kentucky (Culin & Yeargan 1982), as well as in Polish meadows (Kajak 1965) and Swiss cereal fields (Nyffeler & Benz 1979). The goal of this paper is to give insight into the effect of orb weavers in an east Texas cotton field that can be used to adjust the species-specific indices of efficiency used in the tritrophic cotton insect TEXCIM model (Hartstack & Sterling 1988). Studies on the ecology of other spiders occurring in this agroecosystem are presented elsewhere (Nyffeler et al. 1986, 1987a,b,c, 1988a,b; Dean et al. 1987).

Materials and Methods

Study Area. Investigations were conducted during the summer of 1985 (June to mid-September) in a cotton field that received no pesticide applications. This field was located 8 km west of Austonio, Tex., near Crockett in Houston Co., and was bordered by meadows composed of various grasses and low growing annual Dicotyledonae that were mown once during this study. The cotton field had an area of 6.5 ha with 1 m between rows and about 10 cotton plants per meter of row. Cotton (variety CAMD-E) was planted on 27 May and emerged in the first week of June. Parts of this field were heavily infested with weeds (johnsongrass). The field was cultivated on 10 and 29 June. We finished our investigation on 16 September, at which time the cotton had not been harvested.

Evaluation of Numbers of Orb-Weaving Spiders in Cotton. Numbers of orb weavers per square meter were estimated in two ways: through direct counts in the field, and with a D-vac suction machine (D-vac, Riverside, Calif.).

Direct Count. Numbers of small diurnal orb weavers can easily be assessed by counting webs per square meter during daylight hours. On 7 August, small orb weavers were counted in 50 randomly selected $1-m^2$ samples by searching the cotton foliage for webs. Adults of large nocturnal orb-weaving species may be overlooked because many of these spiders remove their webs during the daylight hours and construct retreats under cotton foliage. To accurately estimate their numbers, additional counts were made after dark with a headlamp on 14 and 19 August by walking along

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Spider group	No. spiders/m ² determined by visual counts (\bar{Z})	Estimated cm^2 web area/m ² ground area ^a
,	Mean (% total)	Mean (% total)
Small orb-weavers ^b		
Gea heptagon	0.681 (78.9)	9.66 (57.2)
Others	0.176 (20.4)	2.50 (14.8)
Large orb-weavers ^d		
Acanthepeira stellata	0.003 (0.3)	2.07 (12.3)
Neoscona arabesca	0.003 (0.3)	2.66 (15.7)
Total	0.863 (100)	16.89 (100)

Table 1. Web area versus ground area spun by orb weavers in eastern Texas cotton during their peak numbers, August 1985

^a Orb-web areas calculated as approximation to a circular area: $(\pi)(\bar{D}^2)(\bar{Z})/4$, where \bar{D} is average web diameter in centimeters. ^b Immatures and adults of small-sized species and immatures of

large-sized species.

^cT. laboriosa, U. glomosus, and others.

^d Adults of large-sized species.

cotton rows and recording the numbers of large orb webs hanging across the free space between adjacent rows or in gaps within a row. Each night, spiders were counted along a distance of 500 m (walking speed about 250 m/h), and data were later converted into average number of spiders per square meter. Numbers per square meter of small orb weavers (assessed by day) and of large orb weavers (assessed by night) were combined (Table 1) to provide an estimate of the total number of orb weavers in this cotton field in August.

D-vac Method. Twenty-five D-vac suction samples (Dietrick 1961), each of 1 m of row, were taken weekly over a 14-wk period during the summer of 1985 to obtain estimates of numbers of spiders and of potential prey composition. Details are described in Nyffeler et al. (1987b). Number of spiders per meter of row represents the number per square meter, because the lateral distance between rows was 1 m.

Assessment of Web Size and Catching Area. Because most orb-weaving spiders spin slightly asymmetrical orb webs (Nentwig 1985), it follows that often horizontal diameter is not equal to vertical diameter. In this study, we measured horizontal diameter and vertical diameter of an orb web with a meter stick, and from these two values we calculated the arithmetic mean used as an estimate of parameter \overline{D} (see below). The catching area per spider was calculated as an approximately circular area; the average square centimeters of web area per square meter of ground area was estimated as follows (see Table 1):

cm² web area/m² ground area =
$$\frac{(\pi)(\bar{D}^2)(\bar{Z})}{4}$$
,

where \overline{D} is the average web diameter in centimeters and \overline{Z} is the average number of spiders per square meter (see above).

Evaluation of the Spiders' Prev. Evidence of predation by orb weavers in cotton was obtained by removing arthropod remains from webs. All arthropods found dead in spider webs were considered as prey. Webs were searched for prey during the day and night, and prey items were removed from webs with forceps and preserved in 70% ethyl alcohol. They were later identified and counted under the microscope. Some of the insect carcasses are discarded by the spiders from the web after the meal (Turnbull 1973); these dropped carcasses are usually removed by the scavenging activities of Solenopsis invicta Buren worker ants. Because of different handling times exhibited by the spiders for differing prey taxa, our data may be biased.

Statistical Procedures for Testing Interspecific Differences of Prey Selection. Interspecific differences in the selection of "type" of prey by the investigated orb weavers were tested by computing the proportion of prey items in the four "types" of prey categories-""flying insects;" "jumping in-sects;" "wingless, mobile arthropods;" and "wingless, immobile arthropods"-for each orb-weaver species. Interspecific differences of proportions within a type of prey category were tested by comparing the 0.95 confidence intervals (CI) for proportions using tables in Documenta Geigy (1968); nonoverlapping 0.95 CIs indicate significant differences at the 5% level. However, because confidence intervals do not constitute a rigorous statistical test, those significant differences of proportions discussed in the text were doublechecked using the χ^{2} test for the comparison of proportions.

Results

In this study, orb-weaving spiders were a numerically dominant spider group constituting 10% of all spiders collected during the summer by D-vac (total n = 923; monthly means: June, 15.6%; July, 14.6%; August, 9.3%; September, 3.5%). The taxonomic composition of orb weavers in Texas cotton fields is presented in Dean et al. (1982) and Dean & Sterling (1987). Five species, Acanthepeira stellata (Walckenaer), Neoscona arabesca (Walckenaer), Gea heptagon (Hentz), Tetragnatha laboriosa Hentz, and Uloborus glomosus (Walckenaer), constituted more than 80% of the 88 orb weavers sampled by D-vac in 1985. In early June, when the cotton plants emerged, very few orb-weaving spiders were in the field (0.04 ± 0.04) individuals/m² [$\bar{x} \pm$ SE] in D-vac samples), but a large number already existed in the adjacent meadows (assessed by direct observations and sweep sampling; D.A.D., unpublished data). The same species were found in the meadow as in cotton, with G. heptagon constituting 75% of all orb weavers sampled in the meadow by D-vac (D.A.D., unpublished data). Those found in cotton and the adjacent meadow move readily through the air by ballooning (Dean & Sterling 1985), and it is likely that meadows function as reservoirs for the colonization of cotton fields by orb weavers. Numbers in cotton increased to a maximum in August (0.72 \pm 0.18 individuals/m² [$\bar{x} \pm$ SE] in D-vac samples). The 0.86 individuals/m² (Table 1) that were visually counted is about 20% more than the average numbers assessed by D-vac sampling. In August, these spiders spun an estimated average web area of about 17 cm²/m² ground area (Table 1).

Of these orb weavers, about 99% were smallsized spiders <5 mm long, with *G. heptagon* clearly dominating (Table 1). Large orb weavers, such as adults of *A. stellata* and *N. arabesca* >7 mmlong, constituted <1%.

Locations and relative size of the webs on cotton plants of the five orb-weaver species mentioned above are illustrated in Fig. 1. Considerable differences in habitat use by these spiders were found. The small webs (mean diameter, $4.25 \pm 0.30 [\bar{x} \pm$ SE]; range, 2.5–7.5 cm; n = 21) of G. heptagon are hung almost vertically in plants close to the ground; this species was found in the cotton field in summer as immatures and is reported in the literature to mature in autumn (Sabath 1969). In contrast, U. glomosus constructs delicate, horizontally oriented nets (about 10 cm diameter) in the middle part of the plants, and T. laboriosa spins small to mediumsized webs (about 11 cm diameter) oriented at various angles in the top half of the plant. The large, almost vertically oriented webs (about 30 cm diameter) of adult A. stellata and N. arabesca are normally hung across the free space between adjacent cotton rows and sometimes in gaps within a row. A statistically significant difference was found between average web diameter of large orb weavers (A. stellata, N. arabesca) and smaller orb weavers (G. heptagon, T. laboriosa) (P < 0.001, Mann-Whitney U test, two-tailed).

Gea heptagon and U. glomosus remain on the hub of their webs day and night, whereas the adults of A. stellata and N. arabesca are nocturnal foragers. T. laboriosa were found on the hub of their webs during the night and sometimes during the daylight hours. A. stellata, N. arabesca, and T. laboriosa were observed constructing webs shortly before sundown. G. heptagon was observed spinning webs in the laboratory in the evening or early morning (Sabath 1969). No observations were made on the time of day of web spinning of U. glomosus, but another species of Uloborus was observed building its web 1 or 2 h before dawn (Eberhard 1971). Feeding spiders were found in only 7% of the webs of G. heptagon as assessed in the first half of August during daylight hours.

The prey of the five orb-weaving spiders in cotton consisted of insects (>99%) and spiders (<1%)(Table 2). Aphids were the most abundant prey of all five species (34.6-90%), which is not surprising because these insects also prevailed in D-vac samples (Table 2), indicating that they were a very abundant potential prey on the cotton foliage. Other important prey were small dipterans, cicadellids,



Fig. 1. Relative size and location of the webs (mean values) of five orb-weaving spider species on cotton plants in eastern Texas (web positions of feeding active spiders between mid-July and August 1985).

and hymenopterans. Furthermore, coleopterans were an important component in the prey of A. stellata and N. arabesca. These five insect groups combined made up >90% of the orb weavers' prey. One cotton fleahopper, Pseudatomoscelis seriatus (Reuter), and one adult bollworm moth, Heliothis zea (Boddie), were observed as prey of orb weavers (Table 2), indicating that orb weavers occasionally capture these cotton pests. In the cotton field, evidence of prey selection between the five orb-weaver species was found.

A high proportion (>80%) of flying insects was captured by the two large orb weavers A. stellata and N. arabesca, which spin their strong webs across the free spaces between adjacent cotton rows. The percentages of flying insects in the prey of these two species did not differ significantly (P > 0.05, χ^2). The three smaller orb-weaver species, which spin their orbs within and on the cotton plants, captured a significantly (P < 0.05, χ^2) lower proportion (<50%) of flying insects (Table 3).

Jumping insects and wingless, mobile arthropods each constituted <13% in all five orb weavers' prey (Table 3). Seventeen workers of the red imported fire ant, *S. invicta*, were trapped in webs of *G. heptagon*. Because this spider builds its small orbs attached to cotton leaves close to the ground, ant workers occasionally get stuck in the sticky threads and are wrapped into silk by the spider. In orbs of other spider species positioned on higher levels above ground, *S. invicta* workers were rarely captured; on one occasion a *T. laboriosa* was observed consuming an *S. invicta* worker.

Wingless, relatively immobile insects such as brachypterous aphids constituted a low proportion (<3%) of the prey of the large orb weavers, A. stellata and N. arabesca, but made up a high proportion (>25%) in the smaller orb weavers' prey (Table 3); this difference is statistically significant $(P < 0.05, \chi^2)$.

			Spic	ler		
Prey	A. stellata n = 104, z = 44	N. arabesca n = 22, z = 15	G. heptagon n = 147, z = 111	T. laboriosa n = 41, z = 23	U. glomosus n = 50, z = 16	Estimate % potential prey ^a n = 58,528
Homoptera						
Aphididae, wingless Aphididae, winged Cicadellidae	2.9 31.7 8.7	0 45.5 4.5	25.2 27.2 10.2	43.9 34.1 7.3	68.0 22.0 0	72.2 3.2 4.5
Diptera, small	30.8	4.5	15.6	12.2	4.0	2.1
Hymenoptera						
S. <i>invicta</i> , worker Other, small	1.0 2.9	0 4.5	11.6 4.1	2.4 0	6.0 0	12.6 1.9
Coleoptera						
Curculionidae Scarabaeidae Other	2.9 4.8 6.7	0 22.7 9.1	0 0 0.7	0 0 0	0 0 0	0.1 0 0.3
Heteroptera Lepidoptera, adults Orthoptera	1.9 2.9 ^c 0	4.5 4.5 0	1.4 ^b 0 2.1	0 0 0	0 0 0	$\begin{array}{c} 1.2 \\ \underline{-d} \\ \underline{-d} \end{array}$
Araneae, orb weavers Other	1.0 1.9	0 0	0 1.4	0 0	0	1.6 0
Total	100	100	100	100	100	100

Table 2. Prey (% by number) of five orb-weaving species and their estimated potential prey in a cotton agroecosystem in eastern Texas, summer 1985

n = no. prey items; z = no. spider webs.

^a Based on D-vac sample data; those samples have bias toward some prey types (Pieters & Sterling 1973) but are at least an estimate of potential prey composition.

^b Includes one cotton fleahopper.

^c Includes one *H. zea* adult.

^d Missing in samples because D-vac method not suitable for collecting Lepidoptera or Orthoptera.

Within the cotton foliage, wingless aphids constituted a significantly (P < 0.05, χ^2) higher proportion in the prey spectrum of U. glomosus (>60%), which builds horizontal webs, than in that of G. heptagon (<30%), which builds vertical webs. The percentage of wingless, relatively immobile insects in the prey of T. laboriosa (44%, Table 3), whose webs are oriented at various angles, was between the values of G. heptagon (25%) and U. glomosus (68%) and differed from them significantly (P < 0.05, χ^2).

Discussion

The investigated orb weavers captured a variety of prey taxa characterizing them as generalist predators (Table 2), which is in agreement with previous prey analyses of orb-weaving spiders (LeSar & Unzicker 1978; Nyffeler & Benz 1978; Culin & Yeargan 1982; Nyffeler 1982; Nyffeler et al. 1986, 1987c). One could question if the carcasses of arthropods found in spider webs actually represent the diet or if some of them may have been caught in the webs accidentally. From the point of view of natural pest control, it matters little whether the spider actually feeds on insects caught in webs if the "prey" dies anyway. However, the insect groups which are considered in this paper as prey of orb weavers (such as aphids, cicadellids, dipterans, ants, coleopterans, heteropterans, lepidopterans, and others) have been observed in the field being eaten by orb-weaving spiders (LeSar & Unzicker 1978; Culin & Yeargan 1982; M.N., unpublished data). Thus, we assume that most species of insects found in webs in this study were used as food. According to a field study by Turnbull (1960), a web-building spider accepted 98% of 153 species of insects trapped in the web, demonstrating the low rejection rate of such spiders. Intuitively, many defenses of prey may be largely immobilized by capture in a web.

If we compare the five spiders of this study and their selection of type of prey in relation to the different web positions, web inclinations, and other web characteristics (Fig. 1; Table 3), the following pattern emerges.

Web position was found to be a determinant of prey selection by comparing small orb webs on cotton foliage with the large orb webs spun between cotton rows. We found that orb webs between the rows captured a higher proportion of flying and a lower proportion of wingless, immobile prey.

Orb webs may function as protective barriers (sensu Turnbull 1973) against *S. invicta*, which are aggressive predaceous ants occasionally biting into the legs of spiders (M.N., unpublished data). Web position also was found to be a determinant of prey selection in other studies (Nyffeler & Benz 1978, Olive 1980, Pasquet 1984).

Web orientation may be another factor determining prey selection, evidenced by the observa-

	Large, nocturn	al orb weavers ^a		Small, diurnal orb weavers ^b	
	A. stellata	N. arabesca	G. heptagon	T. laboriosa	U. glomosus
Spider web characteristic	S				
Placement	Between cotton rows	Between cotton rows	Within plant	Within or on plant	Within plant
Inclination	Vertical	Vertical	Vertical	At various angles	Horizontal
Size and strength	Large, strong	Large, strong	Small, delicate	Small, delicate	Small, delicate
Mesh size	Wide meshed	Wide meshed	Close meshed	Close meshed	Close meshed
Thread type	Warps and droplets of gum^c	Warps and cribellum wool ^d			
Type of prey, % (0.95 CI	()				
Flving insects ^e	84.7 (76–91)	95.3 (77-100)	50.0 (41-58)	46.3 (31-63)	26.0(15-40)
Iumping insects ^f	8.7 (4–12)	4.5 (0.1–23)	12.5 (8-19)	7.3 (1-20)	0 (0-7)
Wingless mohile	2.0 (0.2-7)	0 (0-15)	11.8 (7-18)	2.4 (0.1–13)	6.0 (1-17)
Wingless, immobile ^{h}	2.9 (0.6–8)	0 (0-15)	25.7 (19–34)	43.9 (28–60)	68.0 (53-80)
Total	100	100	100	100	100

Table 3. Selection of "type" of prey (in %, with 0.95 CI), in relation to web characteristics by five orb-weaving spiders in a cotton agroecosystem in eastern Texas

ò Ň 0.05 confidence intervals for proportions computed using tables in Documenta Geigy (1908); it CJ Nocturnal as adults, early instars diurnal. ^b May be active day and night, wrap and bite prey. ^c Ecribellate spiders with venom glands, wrap and bite prey. ^d Cribellate spiders wrap prey but do not bite because venom glands are lacking. ^d Cribellate and Aphicidae. Diptera, winged Hymenoptera, Coleoptera, Heteroptera, and Lepidoptera. ^f Cicadellide and Orthoptera. ^g S. tructa workers and spiders. ^h Wingless Aphicidae.

tions that within the cotton plants a significantly $(P < 0.05, \chi^2)$ higher percentage of flying insects were trapped in the vertical G. heptagon webs than in the horizontal U. glomosus webs (50% versus 26%, Table 3). Experiments with artificial traps by Chacon & Eberhard (1980) suggest that insects tend to fly more horizontally than vertically and therefore would be more effectively intercepted in vertical webs. In contrast, horizontal orb webs may be more effective in intercepting wingless, relatively immobile insects (Table 2). How do such wingless, relatively immobile insects fall prey to orb weavers which are "sit-and-wait foragers"? Many wingless aphids located on the undersides of leaves are regularly detached from cotton foliage by wind (M.N., unpublished data). Hunting predators also may disturb them. Sunderland et al. (1986) observed in winter wheat fields that wingless aphid morphs fell from foliage to the ground at a rate of up to >100individuals/ m^2/d . Many of these falling aphids were intercepted in horizontally oriented spider webs. Chacon & Eberhard (1980) suggested that horizontal orb webs may be designed for the capture of prey falling from above.

Mesh size was suggested in the literature to be a determinant of prey selection (Risch 1977, Uetz et al. 1978). In this study, we found that orb weavers spinning close-meshed orbs as well as those spinning wide-meshed orbs (Table 3) caught many small insects of aphid size (>50% in total prey of all five orb-weaver species). No correlation between mesh size and prey size was found by Nentwig (1983) in experiments with artificial webs.

Web strength, which is a function of web size (according to Craig [1987], high-energy-absorbing webs tend to be large), was found to be another determinant of prey selection by orb weavers. Small, delicate orb webs (e.g., those of G. heptagon, U. glomosus, and T. laboriosa) are designed for the interception of small insects and are not suited to capture larger prey such as Lepidoptera and Coleoptera (LeSar & Unzicker 1978, Culin & Yeargan 1982). On the contrary, the large, strong orb webs of adult A. stellata and N. arabesca are designed for the interception of small and large prey. This is consistent with observations of Castillo & Eberhard (1983), who reported that larger orb weavers captured larger prey and a greater variety of prey sizes than smaller spiders.

Coleoptera are excluded as prey of small orb weavers, as observed in *T. labortosa*, which was seen eliminating entangled beetles from the web by violently shaking the web until the beetle fell, by ignoring the beetles until they worked themselves free and could escape, and by cutting the web around an adult beetle and allowing it to drop from the web (LeSar & Unzicker 1978, Culin & Yeargan 1982).

Adult Coleoptera constituted >10% of the prey of the large orb weavers in this study and almost 50% of the prey of *N. arabesca* in Kentucky soybean fields (Culin & Yeargan 1982). These authors assume that the high proportion of Coleoptera in the prey of *N. arabesca* reflects web location and locomotory activity patterns of potential prey.

Noctuid moths also are trapped in these large orb webs (this study, Whitcomb et al. 1963). Large orb weavers were observed in this study feeding on the captured beetles and moths, indicating that those insects actually are used as food. These spiders' efficiency as predators of injurious moths is uncertain because of the ability of those insects to escape from spider webs. Eisner et al. (1964) stated: "Moths, by virtue of the loose scales that cover their wings and bodies, are admirably adapted to elude capture by orb-weaving spiders. Rather than sticking to the web, they may simply lose some of their scales to the viscid threads, and fly on." Robinson & Robinson (1970) estimated from field data that >50% of the moths encountering the webs of a large orb weaver were able to escape; on the other hand, Whitcomb et al. (1963) found many noctuid moths captured in large orb webs in Arkansas cotton fields.

Feeding spiders were found in <10% of the webs of *G. heptagon.* In comparison, spiders were found feeding in about 12% of the webs of *T. laboriosa* in soybeans (LeSar & Unzicker 1978). According to LeSar & Unzicker (1978), those low feeding frequency values suggest that such small orb weavers have low prey capture rates. An immature *G. heptagon* building orbs of only about 4 cm in diameter in August has on the average a 50 times smaller catching area than an adult large-sized orb weaver (e.g., *A. stellata*). However, *G. heptagon*, having reached maturity in fall, build webs of 10–12 cm diameter (Sabath 1969).

In east Texas where small orb weavers predominate, these spiders are primarily predators of smallsized pests such as the cotton aphid, *Aphis gossypii* Glover, and the cotton fleahopper. Orb-weaver predation on these two insects was reported by Kagan (1943) in Texas cotton. Predation of the boll weevil and *Heliothis* spp. by orb-weaving spiders appears to be insignificant because of the apparent inability of small orb weavers to overcome larger pests and because of the low numbers of largesized orb weavers in the cotton fields (see above).

In 1985, all key pests (sensu Bohmfalk et al. 1983) combined constituted only about 1% of the prey of *G. heptagon* and *A. stellata* and were missing in the prey spectra of the other orb-weaver species (Table 2). The low frequency of key cotton pests is in part because of the low densities of those key pests in that area during the summer of 1985 (D.A.D., unpublished data). Conversely, occasional pests (sensu Bohmfalk et al. 1983) such as aphids constituted >30% of the spiders' prey. Predaceous arthropods were rarer (<7%) in the prey of orb weavers except for occasional capturing of *S. in*victa by *G. heptagon*.

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