

McReynolds, C. N. and G. A. Polis. 1987. Ecomorphological factors influencing prey use by two sympatric species of orb-web spiders, *Argiope aurantia* and *Argiope trifasciata* (Araneidae). J. Arachnol., 15:371-383.

## ECOMORPHOLOGICAL FACTORS INFLUENCING PREY USE BY TWO SYMPATRIC SPECIES OF ORB-WEB SPIDERS, *ARGIOPE AURANTIA* AND *ARGIOPE TRIFASCIATA* (ARANEIDAE)

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### ABSTRACT

Two species of orb-web spiders, *Argiope aurantia* Lucas and *Argiope trifasciata* (Forsk.) were used to analyze how accurately spider and web characteristics could predict the type, size, and number of prey captured. The ecomorphological hypothesis proposes that spider and web characteristics determine what subset of the prey population actually will be captured. Prey size and taxa are functions of web height, web diameter and spider size. Mesh density is a poor predictor of these parameters. The number of prey captured by spiders is not correlated with any spider or web characteristic except mesh density of *A. aurantia*. Species-specific differences in spider and web characteristics occurred until both species reached maturity (October). The major differences were that *A. trifasciata* were smaller and matured later than *A. aurantia*. These differences were accompanied by species-specific differences in the size and taxa of prey, but these parameters also converged during October. Differences in the two species may have evolved because of (1) exploitation competition, (2) non-competitive resource partitioning, or (3) interference competition. The diet overlap of the two species was generally high but increased even higher in October. Therefore, it is doubtful that dietary differences were sufficient to prevent exploitation competition.

### INTRODUCTION

The morphology of trophic structures in predators may influence the size and type of prey captured (= ecomorphological hypothesis, see Wiens and Rotenberry 1980). Therefore, species-specific differences in morphology may partition prey between species (Hutchinson 1959; but see Wiens and Rotenberry 1980, 1981). However, the effect of predator morphology on foraging and resource partitioning rarely has been tested on individuals in the field (Wiens and Rotenberry 1980). For spiders, body or leg size may determine the maximum size of prey (Brown 1981; Murakami 1983). In general, overall foraging success apparently is affected by seasonal and yearly changes in both prey characteristics (abundance, size, and taxa) (Riechert and Luczak 1982) and spider characteristics (size, activity, and web) (Riechert and Luczak 1982; Howell and Ellender 1984).

Different species of spiders appear to divide food resources by differences in size, foraging behavior, or spatial and temporal activity patterns (Uetz 1977; Turner and Polis 1979). Differences in foraging behavior, morphology, web

height, and web location may lead to differential capture of prey (Enders 1974; Uetz et al. 1978; Olive 1980, 1981a; Brown 1981). Such species specific differences ultimately may result from competition (Enders 1974; Olive 1980; Brown 1981).

The relationships of spider size and web characteristics to foraging characteristics of two orb-web spiders, *Argiope aurantia* Lucas and *Argiope trifasciata* (Forsk.) were analyzed because these spiders commonly occur in the same habitats and with similar daily activity patterns. Therefore, partitioning of prey resources is predicted (see Brown 1981). The ecomorphological hypothesis was tested to determine which, if any, spider or web characteristics were good predictors of prey characteristics. Temporal and species-specific differences in spider size, web characteristics, and prey captured were described and compared.

### MATERIALS AND METHODS

The study was conducted in old fields and disturbed areas in the Radnor Lake State Nature Area, Nashville, Tennessee, from July through October from 1981-1984. Major components of the vegetation included several species of grass, goldenrod (*Solidago* sp.), ironweed (*Vernonia* sp.), and smartweed (*Polygonum* sp.). Other vegetation included pasture rose (*Rosa* sp.), ragweed (*Ambrosia artemisiifolia*, and thistle (*Cirsium vulgare*).

*Argiope aurantia* and *Argiope trifasciata* (Araneidae) are located easily because of their relatively large size, their habit of sitting in the hub of their large orb-webs (see Reed et al. 1969), the zig-zag stabilimentum at the hub (see Lubin 1974; Tolbert 1975; Horton 1980), and their diurnal habits. The webs of *Argiope* are built in vegetation of old fields and disturbed sites (Enders 1973; Tolbert 1979; Sholes and Rawlins 1979; Olive 1981b). Large prey are wrapped in silk before being carried to the hub while small prey are bitten and carried directly to the hub (see Robinson 1969; Robinson et al. 1969; Hardwood 1974). Maturity is reached in September and October (see Olive 1980; Howell and Ellender 1984). Adult female ( $> 20$  mm) *Argiope* are much larger than adult males ( $< 10$  mm). In September, mature males stop building their own web and are usually located near female webs (Olive 1982). There is only one generation per year: egg production occurs in September and October (Olive 1980; Horton and Wise 1983), the young overwinter in the egg sac, and emergence is in April and May (Tolbert 1977).

The following data were collected: (a) description of the spider (species, total length, abdomen width), (b) web parameters (diameter at the widest point, height from the ground to the hub, and mesh density = number of web spirals per centimeter of web in the middle of the lower spiral zone), and (c) prey captured (prey number per spider per observation period = number of prey captured by a spider during a day of observation; prey size = total length; and prey taxa = order of prey). A prey item was considered captured after it had been wrapped by the spider or carried to the hub. During 1981 and 1982, prey were collected from the webs daily, identified and measured in the laboratory. During 1983 and 1984, prey were identified and measured in the web daily. A bias in the observed number of prey captured per day may occur because prey with a short handling time may be consumed before it was observed or prey with a long handling time may be included in more than one observation period (Fairweather and Underwood 1983). The first bias was possible, but it was unlikely that prey were

Table 1.—Length, taxa, and number of prey captured as a function of spider size class. An one-way ANOVA and a G-test of independence are used to test differences between size classes ( $\bar{X}$  = mean prey length (mm), SD = standard deviation,  $N$  = total number of prey,  $M$  = total number of observations, ns = not significant, OR = Orthoptera, HY = Hymenoptera, CO = Coleoptera, and Other = Other prey items). Means that share a letter are not significantly different (GT2 method,  $P < 0.05$ ).

	Spider Size (mm)										F	
	<i>A. aurantia</i>					<i>A. trifasciata</i>						
	6-10	11-15	16-20	21-25	26-30	6-10	11-15	16-18	19-21	22-25		
Length:												
$\bar{X}$	8.7	12.1	12.7	13.0	12.5	1.58	6.6	9.8	11.7	11.4	11.2	6.60
SD	3.04	6.28	4.28	4.85	5.58	ns	2.06	3.40	3.51	3.81	3.83	<0.001
$N$	7	11	216	235	32		11	39	105	79	5	
							a	ab	c	bc	abc	
Taxa:						G						G
OR	0.0	72.7	31.4	25.5	11.1	30.17	18.2	2.6	18.1	15.2	0.0	32.06
HY	57.1	18.2	35.4	34.0	44.4	<0.01	18.2	51.3	53.3	64.6	20.0	<0.01
CO	14.3	9.1	14.1	23.8	25.0		9.1	20.5	17.1	11.4	40.0	
Other	28.6	0.0	19.1	16.6	19.4		54.5	25.6	11.4	8.9	40.0	
$N$	7	11	220	235	36		11	39	105	79	5	
Number:						G						G
1	100.0	90.0	65.5	64.1	41.2	18.93	88.9	64.3	54.5	61.7	75.0	17.27
2	0.0	10.0	25.7	21.6	35.3	ns	0.0	28.6	34.8	17.0	25.0	ns
3	0.0	0.0	6.8	10.5	11.8		11.1	7.1	7.6	14.9	0.0	
4	0.0	0.0	1.4	3.3	5.9		0.0	0.0	3.0	4.3	0.0	
≥5	0.0	0.0	0.7	0.7	5.9		0.0	0.0	0.0	2.1	0.0	
$M$	7	10	148	153	17		9	28	66	47	4	

included in more than one observation period because we monitored individual prey that spiders captured in previous observations.

All statistical methods, including a t-test for unequal variances ( $t'$ ), were from Sokal and Rohlf (1981). After careful consideration, spider and web characteristics were placed in classes instead presented as continuous data because this more clearly demonstrated important trends. Furthermore, most hypotheses address classes of observations, e.g., low versus high webs, large versus small webs, etc. Some data form natural classes (e.g., orders of prey taxa) and are analyzed more clearly by combining spider and web characteristics into classes for use in contingency tables. Data were pooled from 1981-1984.

## RESULTS

**Ecomorphology.**—*Spider size:* Spider size and web characteristics generally influence the size and type of prey captured. However in some cases, there were no clear patterns. Prey size changed significantly with an increase in spider size classes for *A. trifasciata* but not *A. aurantia* (Table 1). The *A. trifasciata* in the smallest class (6-10 mm) captured significantly smaller prey than spiders in larger classes (16-18 and 19-21) (see Table 1). Significantly different prey taxa were captured by different spider size classes of both species (Table 1). The number of prey captured by different spider size classes was not significantly different for either species (Table 1).

*Web diameter:* For both species, spiders from different web diameter classes captured significantly different sizes of prey (Table 2). *Argiope aurantia* in large

Table 2.—Length, taxa, and number of prey captured as a function of web diameter. An one-way ANOVA and a G-test of independence are used to test differences between web diameter classes ( $\bar{X}$  = mean prey length (mm), SD = standard deviation,  $N$  = total number of prey,  $M$  = total number of observations, ns = not significant, OR = Orthoptera, HY = Hymenoptera, CO = Coleoptera, and Other = Other prey items). Means that share a letter are not significantly different (GT2 method,  $P < 0.05$ ).

	Web Diameter (cm)											
	<i>A. aurantia</i>					<i>A. trifasciata</i>						
	0-20	20-30	30-40	40-50	50-70		0-20	20-30	30-40	40-50		
Length:						F						F
$\bar{X}$	9.5	12.0	13.3	13.1	12.3	4.55	10.0	12.2	10.5	10.3	4.71	
SD	3.10	4.11	4.74	4.83	5.24	$P < 0.01$	3.70	3.75	3.35	3.88	$P < 0.01$	
$N$	24	90	191	135	60		20	75	103	35		
	a	ab	b	b	ab		cd	c	d	d		
Taxa:						G						G
OR	12.5	20.0	29.8	34.8	26.2	45.71	15.0	16.0	10.7	17.1	11.40	
HY	41.7	54.4	38.2	25.2	13.1	$P < 0.001$	50.0	58.7	52.4	54.3	ns	
CO	25.0	12.2	16.8	21.5	27.9		15.0	18.7	13.6	17.1		
Other	20.8	13.3	15.2	18.5	32.8		20.0	7.7	23.3	11.4		
$N$	24	90	191	135	61		20	75	103	35		
Number:						G						G
1	80.0	63.8	63.0	62.1	67.5	12.51	73.3	70.6	56.1	50.0	12.72	
2	20.0	22.4	26.0	23.0	20.0	ns	20.0	15.7	33.3	35.0	ns	
3	0.0	10.3	7.1	12.6	7.5		6.7	9.8	7.6	10.0		
4	0.0	1.7	2.4	2.3	5.0		0.0	3.9	3.0	0.0		
$\geq 5$	0.0	1.7	1.6	0.0	0.0		0.0	0.0	0.0	5.0		
$M$	20	58	127	87	40		15	51	66	20		

web diameter classes (30-40 and 40-50 cm) captured larger prey than spiders in the small web diameter class (0-20 cm), and *A. trifasciata* in a middle web diameter class (20-30 cm) captured larger prey than spiders with larger web diameters (30-40 and 40-50 cm) (see Table 2). Prey taxa also were significantly different for *A. aurantia* using different web diameter classes: the frequency of Hymenoptera decreased, and the frequency of Orthoptera increased with an increase in web diameter (Table 2). There was no significant difference in prey taxa captured by *A. trifasciata* using different web diameter classes (Table 2). The number of prey captured in different web diameter classes was not significantly different for either species (Table 2).

**Web height:** Both prey size and taxa were significantly different for each species using different classes of web height (Table 3). Larger prey were captured by *A. aurantia* in lower web height classes ( $< 100$  cm), but the prey captured by *A. trifasciata* in a middle web height class (40-60 cm) were larger than prey captured by spiders in other web height classes (20-40 and 60-80 cm) (see Table 3). In general, more Orthoptera and fewer Hymenoptera and Coleoptera were captured in lower webs by both species. There was no significant difference in the number of prey captured by spiders using webs of different height (Table 3).

**Mesh size:** The size of prey captured in different mesh size classes was significantly different for *A. trifasciata* but not *A. aurantia* (Table 4). Mean prey size decreased with increased mesh density for both species, but the high variance in *A. aurantia* obscured statistical significance. Prey taxa were not significantly different for either species using different mesh size classes (Table 4). The number of prey captured in webs of different mesh size classes was significantly different

Table 3.—Length, taxa, and number of prey captured as a function of web height. An one-way ANOVA and a G-test of independence are used to test differences between web height classes ( $\bar{X}$  = mean prey length (mm), SD = standard deviation,  $N$  = total number of prey,  $M$  = total number of observations, ns = not significant, OR = Orthoptera, HY = Hymenoptera, CO = Coleoptera, and Other = Other prey items). Means that share a letter are not significantly different (GT2 method,  $P < 0.05$ ).

	Web Height (cm)										
	<i>A. aurantia</i>						<i>A. trifasciata</i>				
	20-40	40-60	60-80	80-100	>100		20-40	40-60	60-80	80-120	
Length:						F					F
$\bar{X}$	13.4	13.1	12.5	13.3	10.1	4.14	7.9	11.8	10.3	10.8	3.15
SD	4.80	4.75	4.54	4.68	4.48	$P < 0.01$	3.50	3.79	2.97	3.63	$P < 0.05$
$N$	66	183	157	54	41		13	119	65	35	
	a	a	a	a	b		c	d	c	cd	
Taxa:						G					G
OR	44.9	36.1	20.4	19.2	2.5	55.88	9.1	22.0	3.0	5.9	30.87
HY	20.3	30.4	45.9	34.6	42.5	$P < 0.001$	36.4	55.1	59.1	52.9	$P < 0.001$
CO	14.5	16.5	14.6	30.8	15.0		18.2	7.6	24.2	29.4	
Other	20.3	17.0	19.1	15.3	40.0		36.4	15.3	13.6	11.8	
$N$	69	194	157	52	40		11	118	66	34	
Number:						G					G
1	74.5	63.8	68.2	58.3	52.2	17.87	62.5	68.3	58.1	40.0	16.43
2	12.8	25.2	21.8	33.3	26.1	ns	12.5	23.2	32.6	35.0	ns
3	6.4	9.4	7.3	8.3	8.7		25.0	3.7	7.0	25.0	
4	4.3	0.8	1.8	0.0	13.0		0.0	3.7	2.3	0.0	
$\geq 5$	2.1	0.8	0.9	0.0	0.0		0.0	1.2	0.0	0.0	
$M$	47	127	110	36	23		8	82	43	20	

for *A. aurantia* but not *A. trifasciata* (Table 4). More prey per spider were captured by *A. aurantia* using smaller mesh size classes (Table 4).

There was not a close correlation (correlation coefficient = 0.15-0.46) between different spider and web characteristics. Therefore, the effect of a particular characteristic on prey capture was largely independent of other spider or web characteristics.

**Temporal differences.**—*Spider size:* Spider size, web characteristics, and prey size and taxa changed weekly. Females of both species grew over most of the summer (Fig. 1a). However, spider length showed no significant increase after September 1 for *A. aurantia* and after September 16 for *A. trifasciata* (Fig. 1a) suggesting that these spiders were either adult or penultimate females.

*Web characteristics:* Web diameters of *A. aurantia* ( $F(4,361) = 13.52 P < 0.001$ ) and *A. trifasciata* ( $F(4,153) = 8.25 P < 0.001$ ) changed significantly over time (Fig. 2a). Mean web diameter of *A. aurantia* was largest during early September but that of *A. trifasciata* continually increased to the end of the season. Mean web height significantly increased over time for *A. trifasciata* ( $F(4,157) = 6.372 P < 0.001$ ) but not *A. aurantia* ( $F(4,370) = 1.13$  ns) (Fig. 2b).

*Prey:* The mean length of prey captured by all spiders showed a significant increase over time for *A. trifasciata* ( $F(4,234) = 11.27 P < 0.001$ ) but not *A. aurantia* ( $F(4,537) = 1.43$  ns) (Fig. 1b). The identity of prey changed significantly over time for both species (Table 5). The frequency of Coleoptera was high during early September for *A. aurantia*, and the frequency of Hymenoptera increased over time for both species (Table 5). Coleoptera, Hymenoptera, and Orthoptera were the major prey types (Table 5). The major Coleoptera was the

Table 4.—Length, taxa, and number of prey captured as a function of web mesh size. An one-way ANOVA and a G-test of independence are used to test differences between mesh size classes ( $\bar{X}$  = mean prey length (mm), SD = standard deviation,  $N$  = total number of prey,  $M$  = total number of observations, ns = not significant, OR = Orthoptera, HY = Hymenoptera, CO = Coleoptera, and Other = Other prey items). Means that share a letter are not significantly different (GT2 method,  $P < 0.05$ ).

	Mesh (/cm)								F
	<i>A. aurantia</i>			<i>A. trifasciata</i>					
	1-2	3-4	5-6	1-2	3-4	5-6	>6		
Length:				F					F
$\bar{X}$	12.6	11.3	7.6	2.58	12.6	9.3	8.3	7.0	3.12
SD	6.45	5.16	2.07	ns	4.07	4.40	3.17	2.65	$P < 0.05$
$N$	66	38	7		8	45	14	9	
					a	ab	ab	b	
Taxa:				G					G
OR	15.7	12.8	28.6	9.62	0.0	15.9	7.1	0.0	15.42
HY	45.7	28.2	57.1	ns	37.5	50.0	35.7	22.2	ns
CO	14.3	12.8	0.0		37.5	18.2	14.3	11.1	
Other	24.3	46.2	14.3		25.0	15.9	42.9	66.7	
$N$	70	39	7		8	44	14	9	
Number:				G					G
1	50.0	66.7	100.0	21.05	85.7	69.7	72.7	66.7	4.04
2	18.8	29.6	0.0	$P < 0.001$	14.3	24.2	18.2	16.7	ns
3	15.6	0.0	0.0		0.0	3.0	9.1	16.7	
4	15.6	0.0	0.0		0.0	0.0	0.0	0.0	
$\geq 5$	3.1	3.7	0.0		0.0	3.0	0.0	0.0	
$M$	32	27	7		7	33	11	6	

soldier beetle, *Chauliognathus pennsylvanicus* (Cantharidae) (82% of Coleoptera). The major Hymenoptera was the honeybee, *Apis mellifera* (49%). Other families of Hymenoptera (e.g., Vespidae) that commonly visit flowers were also important prey items. Two families of Orthoptera were captured: Acrididae and Tettigoniidae. Lepidoptera were occasionally important in *A. aurantia*'s diet.

**Comparisons of the two species.**—*Body size:* Although there were species-specific differences in size, web characteristics, temporal patterns, and prey size and taxa there were also many similarities. *Argiope aurantia* was significantly larger than *A. trifasciata* as adult and penultimate females (Table 6), and always significantly larger during the same biweekly period (July F(1,8) = 11.86  $P < 0.01$ , August F(1,25) = 18.23  $P < 0.001$ , Sept. 1-15 F(1,144) = 103.42  $P = 0.001$ , Sept. 16-30 F(1,137) = 28.09  $P < 0.001$ , Oct. 1-15 F(1,111) = 51.60  $P < 0.001$ , and Oct. 16-30 F(1,34) = 5.88  $P < 0.05$ ; Fig. 1a). The largest difference in length was during early September where *A. aurantia* had reached adult size, but *A. trifasciata* were still immature.

*Web characteristics:* Web height of *A. aurantia* and *A. trifasciata* was not significantly different (Table 6). Web diameter was significantly different with *A. aurantia* building a larger web (Table 6). Webs of *A. aurantia* were significantly higher and larger than webs of *A. trifasciata* during early periods but converged towards the end of the season (Web diameter: July-August  $t' = 2.73$   $P < 0.05$ , Sept. 1-15 F(1,114) = 25.69  $P < 0.001$ , Sept. 16-30 F(1,156) = 5.82  $P < 0.05$ , Oct. 16-30 F(1,166) = 0.98 ns, Oct. 16-30 F(1,58) = 0.12 ns; and Web height: July-August  $t' = 3.44$   $P < 0.01$ , Sept. 1-15 F(1,116) = 8.16  $P < 0.01$ , Sept. 16-30 F(1,156) = 0.02 ns, Oct. 1-15 F(1,168) = 0.18 ns, and Oct. 16-30 F(1,58) = 0.09 ns; Fig. 2).

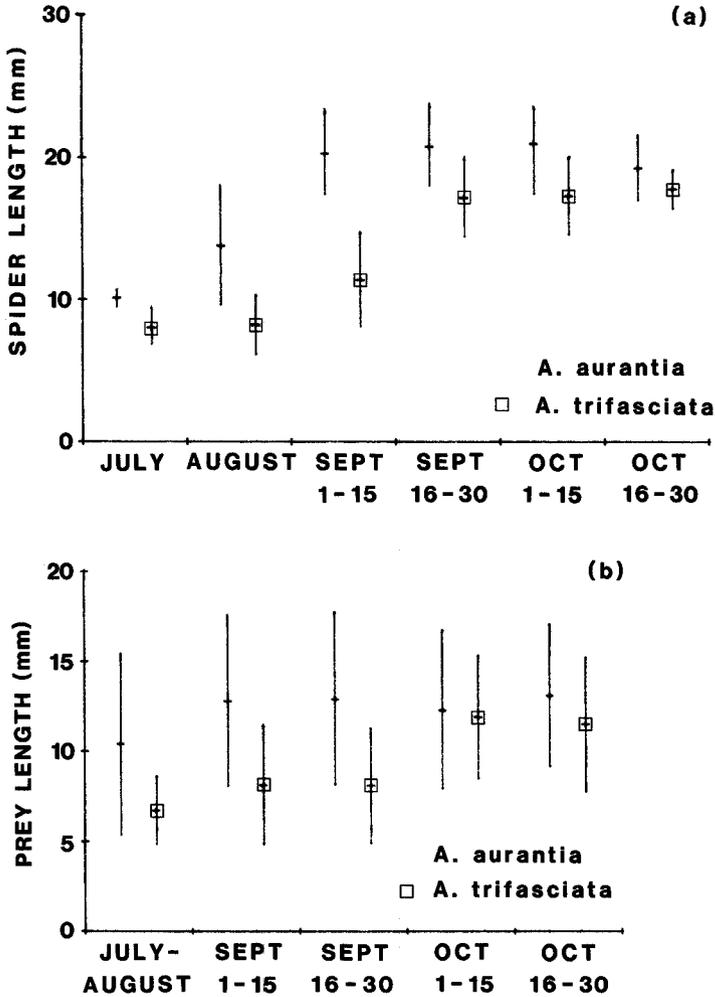


Fig. 1.—Mean ( $\pm 1$  standard deviation) (a) spider and (b) prey length of *Argiope* during biweekly periods. See text for comparisons over time and among species.

*Prey*: The length of prey captured by *A. aurantia* was significantly larger than that captured by *A. trifasciata* (Table 6). *Argiope aurantia* took significantly larger prey than *A. trifasciata* during early periods but prey sizes converged during October when almost all spiders were adults (July-August  $t = 3.00$   $P < 0.05$ , Sept. 1-15  $F(1,116) = 15.55$   $P < 0.001$ , Sept. 16-30  $F(1,211) = 19.00$   $P < 0.001$ , Oct. 1-15  $F(1,244) = 0.59$  ns, and Oct. 16-30  $F(1,95) = 3.70$  ns; Fig. 1b). Significantly different prey taxa were captured by *A. aurantia* and *A. trifasciata* overall and through most of the biweekly periods until late October (Table 5). There was a tendency for *A. aurantia* to capture more Orthoptera and *A. trifasciata*, more Hymenoptera.

### DISCUSSION

Web-building spiders are a good example of sit-and-wait predators (Schoener 1969; Riechert and Luczak 1982). These spiders remain in one site until prey

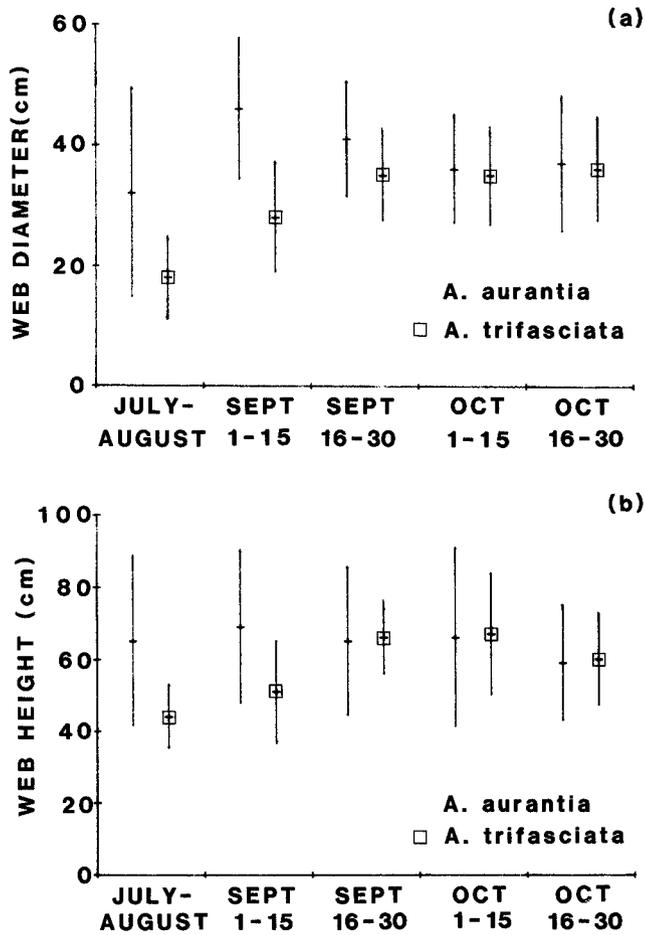


Fig. 2.—Mean ( $\pm 1$  standard deviation) (a) web diameter and (b) height of *Argiope* during biweekly periods. See text for comparisons over time and among species.

move within attack range and thus cannot influence the number and type of prey encountering the web except by placement of the web in a good micro-habitat (Turnbull 1973). Therefore, spiders should select web-sites or heights that allow the greatest encounter and capture rates (e.g., near flowering plants) (Riechert 1974, 1976; Riechert and Tracy 1975; Uetz et al. 1978; but see Enders 1973, 1977; Colebourn 1974; Schoener and Toft 1983). The best method to evaluate web-site quality is a bioassay of prey capture at different sites (see Castillo and Eberhard 1983).

In summary, prey size and taxa are functions of web height, web diameter and spider size. Mesh density is a poor predictor of these parameters. The number of prey captured by spiders is not correlated with any spider or web characteristic except mesh density of *A. aurantia*.

Proponents of the ecomorphological hypotheses have proposed that spider and web characteristics determine which subset of the prey population actually will be captured (Olive 1980, 1981a; Brown 1981; Murakami 1983). During this research more Orthoptera were captured at low web sites and more Hymenoptera and Coleoptera, at higher web sites by both species (also see Uetz et al. 1978; Olive

Table 5.—Taxa of prey captured by *A. aurantia* (A.a.) and *A. trifasciata* (A.t.) over time with all years combined. The relative frequency of prey is identified to order for each time period. All periods are biweekly except July-August. A G-test of independence is used to test differences between time periods and species ( $N$  = total number of prey, ns = not significant, HY = Hymenoptera, OR = Orthoptera, CO = Coleoptera, LE = Lepidoptera, DI = Diptera, HE = Hemiptera, HO = Homoptera, ME = Mecoptera, Other = Other insects, and AR = Araneae).

	Sept. 1-15		Sept. 16-30		Oct. 1-15		Oct. 16-30		Total	
	A.a.	A.t.	A.a.	A.t.	A.a.	A.t.	A.a.	A.t.	A.a.	A.t.
Taxa:										
CO	38.0	15.4	15.1	21.7	9.9	17.2	7.4	11.6	21.7	15.9
HY	14.1	30.7	36.6	47.8	50.4	59.4	51.9	53.6	33.2	54.3
OR	27.1	0.0	30.2	0.0	23.1	13.3	25.9	23.2	26.4	14.2
LE	6.8	0.0	2.9	0.0	0.8	1.6	0.0	0.0	4.2	0.4
DI	4.2	23.1	4.4	4.3	0.8	3.1	3.7	1.4	3.4	3.8
HE	2.1	7.7	2.0	0.0	5.0	2.3	3.7	2.9	2.7	2.9
HO	1.6	0.0	0.0	17.4	0.0	0.8	0.0	1.4	0.7	3.3
ME	2.1	15.4	2.4	4.3	0.8	0.8	7.4	4.3	2.2	2.9
Other	3.6	7.7	5.9	0.0	5.0	1.6	0.0	1.4	4.5	1.7
AR	0.5	0.0	0.5	4.3	4.1	0.0	0.0	0.0	1.3	0.4
$N$	192	13	205	23	121	128	27	69	554	239
Differences between species:										
G	23.02		39.65		20.85		2.53		56.07	
P	<0.01		<0.001		<0.05		ns		<0.001	
Temporal Differences:	<i>A. aurantia</i> G = 116.19 $P < 0.001$									
	<i>A. trifasciata</i> G = 56.65 $P < 0.01$									

1980; Pasquet 1984a). This suggests that orb-web spiders may influence the type of prey encountered by use of different web sites (see Tolbert 1979; Olive 1980; Biere and Uetz 1981; Greenstone 1984). Larger webs encounter more and larger prey by either covering more area (Olive 1980) or being positioned in the path of large and active prey (Uetz et al. 1978; Howell and Ellender 1984). In this study, larger prey were captured by *A. aurantia* with larger webs. However, smaller prey were captured by *A. trifasciata* with larger webs. Furthermore, overall capture rates of prey by both species were not influenced by web diameter. The encounter rate with smaller prey may increase with denser mesh (Uetz et al. 1978; Murakami 1983). The decrease in mean prey size captured by *A. trifasciata* with an increase in mesh density tends to support this hypothesis; however, it does not explain why (for *A. aurantia*) there was no change in prey size, and there was a decrease in the overall capture rate with an increase in mesh density.

Larger and more dense webs may retain large or clumsy prey (e.g., Orthoptera) longer thus decreasing the probability of escape (Olive 1980, 1981a). Another predator, an antlion, attempted to capture larger ants when its pit was larger (Heinrich and Heinrich 1984). Mean prey size of *A. aurantia* and *A. trifasciata* increased with an initial increase in web diameter, after which there was an apparent asymptote in *A. aurantia* or even a decline in *A. trifasciata* such that larger webs did not capture larger prey. Large Hymenoptera were captured less frequently by *A. aurantia* in large webs possibly because Hymenoptera may avoid or escape larger webs better than other prey (see Olive 1980). Furthermore, no increase in prey size with mesh density suggests that mesh size does not improve chances of retaining prey.

Table 6.—Mean adult spider length, prey length, web height, and web diameter. ( $\bar{X}$  = mean, SD = standard deviation, and  $n$  = sample size). A one-way ANOVA is used to test the differences between species (ns = not significant).

Species		Spider Length (mm)	Prey Length (mm)	Web Height (cm)	Web Diameter (cm)
<i>A. aurantia</i>	$\bar{X}$	20.6	12.7	66	41
	SD	2.63	4.62	21.2	10.0
	$n$	312	542	353	350
<i>A. trifasciata</i>	$\bar{X}$	17.5	11.0	64	35
	SD	2.39	3.43	14.6	8.0
	$n$	110	239	137	137
Differences between species:					
	F	119.2	23.3	0.90	42.6
	P	<0.001	<0.001	ns	<0.001

Growth may increase efficiency at handling prey (Olive 1980; Riechert and Luczak 1982) and thus spiders may capture larger prey as they increase in size (Murakami 1983; Brown 1981). This is a general trend observed in other predators (Turner 1979; Mittelbach 1981; Werner and Mittelbach 1981; Polis 1984 and included references). In the present study, prey size generally increased with size of *A. trifasciata*, but smaller individuals of *A. aurantia* occasionally captured large prey making it unclear exactly how spider size affects size of prey captured.

**Temporal differences.**—Temporal (weekly or yearly) changes in foraging success may be affected by several factors. For example, large prey are most available in late summer or early fall (Olive 1980, 1981b; Pasquet 1984b). Insects feeding on nectar and pollen (e.g., cantharid beetles, bees, and wasps) increase locally when plants are in flower (Olive 1980). Flowering phenology and subsequent insect activity may explain the increase in Coleoptera captured by *A. aurantia* during early September and the increases in Hymenoptera captured by *A. aurantia* and *A. trifasciata* in October. Other habitat changes may result in seasonal changes in *Argiope* diet (Olive 1980; Brown 1981; Horton and Wise 1983; Howell and Ellender 1984).

Temporal changes in spider size and web characteristics affect foraging. The growth of *A. trifasciata* partially explains the increase in prey size and changes in prey taxa captured over time. Increases in Hymenoptera in the diet over time are related to seasonal increases in web height of *A. trifasciata*, and the decrease in web diameter of *A. aurantia*. Therefore, changes in web characteristics increase the frequency of encounter and capture of a particular prey. Alternately, environmental variability is known to influence prey availability and temporal differences in diet (see Wiens 1977). Both diet and web characteristics reflect changes in the preferred habitat over time (Brown 1981; Howell and Ellender 1984). *Argiope* spp. are flexible in habitat use and occasionally shift habitats in response to increased prey availability (Olive 1980; Brown 1981). For example, as *A. trifasciata* grows it moves from a low grassy site to high sites with many herbs in flower (see Olive 1980). Such movement not only increases web height but also allows the capture of more Hymenoptera and Cantharidae. Thus dietary or web changes may be a function of habitat rather than diet being a direct function of web characteristics.

**Resource partitioning.**—Several different selective forces have been hypothesized as important in the evolution of species-specific differences. (1) Exploitation competition causes differences in the use of prey (Abrams 1975; Thomson 1980) or habitat (Schoener 1974). (2) Differences in diets may result from non-competitive partitioning of resources due to autecological adaptation to different habitats or foraging methods (Wiens 1977; Bloom 1981). (3) Interference competition can produce in temporal, spatial, or behavioral avoidance of the dominant species by the subordinate species (Case and Gilpin 1974; Carothers and Jaksic 1984; Polis and McCormick 1987).

Comparisons between *Argiope* spp. showed differences in size, web characteristics, and prey. *Argiope aurantia* captured larger prey and more Orthoptera than did *A. trifasciata*; *A. trifasciata* captured more Hymenoptera than *A. aurantia*. Web and habitat differences are known to contribute to dietary differences in spider species (see Enders 1974; Brown 1981; Riechert and Cady 1983; Wise and Barata 1983).

Dietary differences also were influenced by temporal differences in spider and web characteristics. *Argiope trifasciata* captured smaller prey than those captured by *A. aurantia* until October when both species were mature resulting in both spider and prey size convergence (see Turner and Polis 1979; Polis 1984). Dietary convergence in October was influenced further by the observed convergence in web characteristics. Finally, use of the same habitat(s) (with prey availability similar for both species) may also contribute to the October convergence in diet and web characteristics.

Both species ate the same major taxa of prey. Therefore, it is doubtful that dietary differences are large enough to prevent exploitation competition. For this and other reasons, it is not clear if exploitation competition even occurs between *A. aurantia* and *A. trifasciata* (see Horton and Wise 1983; McReynolds and Polis in prep.). The observed dietary differences appear to be due to varying non-competitive abilities of *A. aurantia* and *A. trifasciata* to handle and capture different prey (Olive 1980, 1981a) or to autecological differences in habitat use and foraging methods (see Wiens 1977; Bloom 1981). Alternately, interference by the larger *A. aurantia* can exclude *A. trifasciata* from preferred habitats and prey (Case and Gilpin 1974; Carothers and Jakosic 1984; McReynolds in prep.). Under these conditions, a temporal shift may occur because the larger *A. aurantia* can effectively exclude *A. trifasciata*. Further research is needed to separate these hypotheses.

#### ACKNOWLEDGMENTS

This paper was part of the first author's dissertation. We would like to thank to William Eickmeier, David McCauley, Susan Brawley, Molly Miller, and three reviewers; their comments greatly improved the manuscript. We would also like to thank Lynne Born, Kelley Cox, Denise Due, Sharon McCormick, Chris Myers, Ken Schulteure, and David Sissom for their assistance in the field. We appreciate the assistance of James C. Cokendolpher in the identification of the spiders. We appreciate the advice of David McCauley on the statistical methods used. We received support from Sigma Xi and Vanderbilt University Dissertation Improvement Grant for this research. The research was conducted at Radnor Lake State Nature Area, Nashville, Tennessee.

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