

# Partitioning of Niches Among Four Species of Orb-Weaving Spiders in a Grassland Habitat

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Environ. Entomol. 38(3): 651–656 (2009)

**ABSTRACT** Partitioning of niches can play an important role in structuring faunal communities. We tested the hypothesis that differences between four species of orb-weaving spiders (Araneidae) in body size and the structure and position of their webs resulted in their partitioning the available prey. The study species are sympatric in a grassland habitat and included *Argiope trifasciata* (Forskål), *Cyclosa turbinata* (Walckenaer), *Mangora gibberosa* (Hentz), and *Neoscona arabesca* (Walckenaer). The spider species differed in body size, web diameter, height of web above the ground, spacing of mesh within webs, and the type of plant to which the web was attached. The spider species had a generalist diet and captured prey of multiple trophic levels. Nevertheless, the hypothesis was supported: the spider species differed in the types of prey that they captured. Partitioning of the available prey was influenced by body size, with larger spiders capturing larger prey, but not by the structure or position of their webs. Differences between spider species in niche may reduce competitive interactions and allow them to coexist in sympatry.

**KEY WORDS** Araneidae, *Argiope trifasciata*, *Neoscona arabesca*, *Cyclosa turbinata*, *Mangora gibberosa*

Species of the same guild may coexist in sympatry if they partition their niche, such as by using different foraging strategies (Denno et al. 1981, Schluter 1986, Herder and Freyhoff 2006, Schwemmer et al. 2008). Spiders living in the same habitat typically partition their niches along one or more of the following niche axes: prey type (Harwood et al. 2003), spatial position of the web (Enders 1974, Olive 1980, Brown 1981, Horton and Wise 1983, Heberstein 1998, Cumming and Wesolowska 2004), and phenology (Spiller 1984, McReynolds and Polis 1987). Species of orb-weavers in particular may compete for resources because they are sit-and-wait predators, often are nocturnal, and may encounter the same types of prey (Spiller 1984, Nyffeler and Benz 1989). However, differences between orb-weaving species in morphology and web structure, such as spacing of mesh and web size, may result in their capturing different types or numbers of prey (Risch 1977, Uetz et al. 1978, Culin and Yeorgan 1982, McReynolds and Polis 1987, Nyffeler et al. 1989). Orb-weaving species also may differ in how their webs are positioned within vegetation, and for that reason, species diversity is highest in habitats that are architecturally or floristically diverse (Duffy 1962, Robinson 1981, Uetz 1991, Weeks and Holtzer 2000, Langellotto and Denno 2004, Beals 2006).

In this study, we tested the hypothesis that four species of orb-weaving spiders (Araneidae) of a grassland habitat partition the available prey. We collected spiders of the species *Argiope trifasciata* (Forskål), *Cyclosa turbinata* (Walckenaer), *Mangora gibberosa* (Hentz), and *Neoscona arabesca* (Walckenaer), and the prey captured in their webs, in study plots that represented a range of successional ages (after cultivation).

## Materials and Methods

**Study Site.** We conducted our study over a 2-yr period (2006–2007) at Phillips Tract (Champaign Co., IL), a 52-ha former farm that is a University of Illinois natural area. Our  $\approx 3.3$ -ha study area was divided into six adjacent  $\approx 0.55$ -ha plots (22 by 200 m) that were oriented east–west and separated from one another by 5-m-wide buffer strips. Each plot had been alternately cultivated with soybeans and corn once every 6 yr and left fallow in the interim. Thus, in any particular year, there was one plot that was planted in corn or soybeans and one plot each that had been fallow for 1, 2, 3, 4, and 5 yr. During fallow years, plots were colonized by a variety of native and exotic plant species. We included all of the plots, representing all ages of succession, to enhance variation in the diversity of plant species and plant architecture. For the purposes of this study, however, we do not consider individual plot or

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successional age as explanatory variables in statistical analyses but rather accumulate the data across study plots.

We assessed the relative abundance of plant species in study plots by visually estimating the area that they covered within 25 quadrats ( $0.25 \text{ m}^2$ ) that were positioned haphazardly within each study plot on 14 July and 15 August 2006 and 2 July, 2 August, and 2 September 2007. We identified cover plants as annual/biennial forbs,  $C_3$  grasses,  $C_4$  grasses, woody plants, perennial forbs, and herbaceous legumes (unpublished data). The dominant plant was *Solidago altissima* L. (tall goldenrod), followed by other perennial forbs, such as *Trifolium pratense* L., and *Asclepias syriaca* L., which together represented  $>70\%$  of the groundcover in some plots. Goldenrod grew clonally, rhizomes produced multiple ramets, and it formed a dense monoculture in study plots that had been fallow for  $>2$  yr.

**Abundance of Orb-Weaving Spiders.** We measured the relative abundance of orb-weaving spider species in the study plots two or three times per year (14 July and 15 August 2006; 2 July, 2 August, and 2 September 2007). We included two life stages of spiders in our study, juveniles (sex undetermined) and adult females, because juvenile spiders often capture different types of prey than do adults (Howell and Ellender 1984, Spiller 1984). We initially included data on both early- and late-instar juveniles, but preliminary analyses indicated that they did not differ in characteristics of their web. We therefore combined the data for juveniles into a single category. Adult males were not included because they often do not spin webs (Horton and Wise 1983; M.L.R., unpublished data). All of the orb-weaving spider species at our study site were primarily nocturnal (Moulder 1992; M.L.R., unpublished data), but some individuals remain in their webs during the day. We estimated their relative abundance by collecting spiders from webs within the same 25 quadrats mentioned above. We removed spiders from each web with forceps and preserved them in 70% ethyl alcohol. We also determined the relative abundance of spider species in study plots at night (beginning 0.5 h after sunset on each sampling date) by walking down the center of plots, lengthwise, while holding a 1-m-long pole horizontally and collecting spiders from webs that fell within that swath. We identified juvenile and adult female spiders to species (following Moulder 1992) and estimated body size by measuring the length of the cephalothorax to the nearest 0.25 mm using a fine-scale ruler.

**Characteristics of the Web.** We characterized the structure of webs of all spiders that were collected by measuring the height of the hub above the ground and web diameter (averaged height and width). We took multiple measurements of the spacing of spiral threads (hence referred to as "mesh") within webs and assigned the median to one of the following size classes (following Nentwig 1983 and Nyffeler et al. 1989): 1 = close (0–3 mm), 2 = intermediate (3–6 mm), or 3 = wide ( $>6$  mm). We also recorded the species of the plant or plants to which webs were attached as either

goldenrod (the dominant perennial), forbs other than goldenrod (hence referred to as "forbs"), grasses, or multiple plant types (web attached to plants in multiple categories).

**Prey Captured by Spiders.** We removed arthropod remains from webs of all of the spiders that were collected, preserved them in 70% ethyl alcohol, identified them to family, and measured their body length. We assumed that all arthropods in webs had been fed on by the spider, which was likely. However, these data undoubtedly are incomplete because spiders often remove the remains of prey from their webs after feeding (Turnbull 1973, Olive 1980). We also estimated the general abundance of potential prey within study plots in July 2006 and July and August 2007 by sampling vegetation in 10 quadrats ( $0.25 \text{ m}^2$ ; haphazardly positioned) in each plot with a leaf blower (model BG 55; Stihl, Waiblingen, Germany) that was modified to serve as a vacuum sampler (air flow rate,  $700 \text{ m}^3/\text{h}$ ; velocity, 63 m/s). Arthropods were captured by fitting an organdy bag ( $\approx 3.8$ -liter volume; 0.2 mm mesh) over the end of the intake tube. Arthropods were killed by placing the bags in a freezer.

**Data Analyses.** For all of the analyses described below, means ( $\pm$ SE) were calculated by totaling data within years and then averaging across years. Differences between spider species and life stages (juvenile versus adult) in body size were tested by analysis of variance (ANOVA; PROC GLM; SAS Institute 2002), blocked by year, including the interaction term. Differences between species and life stages in characteristics of the web and the size of captured prey were tested by analysis of covariance (ANCOVA; PROC GLM; SAS Institute 2002), with body size of the spider as the covariate, blocked by year, with the interaction. We tested differences between means initially with full ANOVA/ANCOVA models, but eliminated insignificant interactions and random effects step-wise from models, starting with highest order interactions, and leaving only significant terms (see Milliken and Johnson 1984). Some data were missing because we could not measure body size of spiders and prey and characteristics of the web for each spider (some spiders escaped, were mangled during capture, or dried out before measurements were taken and webs were not always intact), which accounts for reduced degrees of freedom. Differences between individual means were tested with Fisher least significant difference (LSD) means separation test (Sokal and Rohlf 1995).

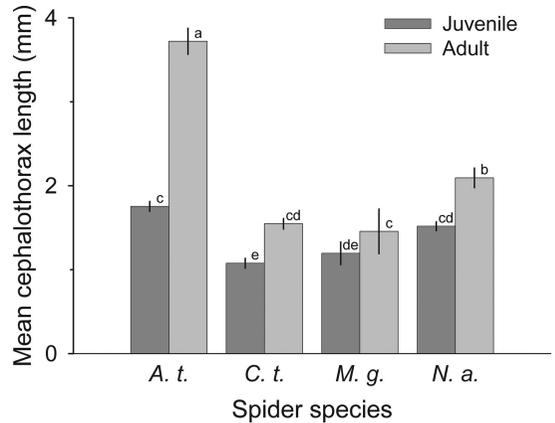
We used a  $\chi^2$  contingency test to determine whether individuals of different life stages and species differed in the type of vegetation to which their webs were attached, in the type of prey that were captured (assessed at the level of insect order because too few specimens were collected to assess at the level of insect family), or whether the prey they captured differed from a random sampling of available prey (by comparing with relative abundance of prey in the habitat; see Zar 1999). We included in that analysis only the seven most abundant insect orders and sub-

**Table 1.** Abundance per year, total no. (with percentage of the grand total), and mean ( $\pm$ SE, across years) no. of orb-weaving spiders of four species and two life stages that were collected from webs in study plots during five sampling periods in 2006–2007

Species and life stage	Abundance		N (%)	Mean (SE)
	2006	2007		
<i>Argiope trifasciata</i> adult	3	63	66 (12.7)	33.0 (30.0)
<i>A. trifasciata</i> juvenile	67	72	139 (26.8)	69.5 (2.5)
<i>Cyclosa turbinata</i> adult	45	36	81 (15.6)	40.5 (4.5)
<i>C. turbinata</i> juvenile	40	12	52 (10.0)	26.0 (14.0)
<i>Mangora gibberosa</i> adult	1	20	21 (4.05)	10.5 (9.5)
<i>M. gibberosa</i> juvenile	6	14	20 (3.85)	10.0 (4.0)
<i>Neoscona arabesca</i> adult	6	28	34 (6.55)	17.0 (11.0)
<i>N. arabesca</i> juvenile	54	52	106 (20.4)	53.0 (1.0)
Total	222	297	519	

orders and excluded the spider *M. gibberosa* because too few prey were collected for that species.

We determined whether the body size of spiders, and their web structure, influenced the body size of prey and capture of two types of prey (including only the two most abundant types of prey, homopterans and dipterans; see Results) with Akaike’s information criterion adjusted for small sample sizes ( $AIC_c$ ) and Akaike weights ( $w_i$ ; Burnham and Anderson 2002; Anderson 2008). This information-theoretic approach identifies the most parsimonious models from a set of candidate models, given maximized log-likelihood of the fitted model. The  $\Delta AIC_c$  value for each model is the level of empirical support relative to all models in the candidate set: models with  $\Delta AIC_c$  values of 0–2 have strong empirical support, those with values 4–7 have weaker support, those with values 9–14 have little support, and those with values >14 have no support. The weight of each model is the probability that it is the best model and varies from one (complete support) to 0 (no support). The relative importance of each predictor variable also can be calculated by summing the weight of each model in which the variable appears and varies from 1 (complete support) to 0



**Fig. 1.** Mean cephalothorax length ( $\pm$ SE) of juvenile and adult female orb-weaving spiders of the species *A. trifasciata* (*A. t.*), *C. turbinata* (*C. t.*), *M. gibberosa* (*M. g.*), and *N. arabesca* (*N. a.*). Means with different letters are significantly different (Fisher LSD means separation test,  $P < 0.05$ ).

(no support).  $R^2$  values indicate how well each model fits the dataset and indicates its relative usefulness as a tool for prediction. Regression coefficients ( $\pm$ SE) indicate whether predictor variables are positively or negatively associated with the response variable.

**Results**

**Abundance of Orb-Weaving Spiders.** We captured 519 spiders during 2006 and 2007 (Table 1), with the most abundant being juveniles of the species *A. trifasciata* and *N. arabesca* and adult *C. turbinata* and *A. trifasciata*. Most spiders (89.2%) were captured at night, but spiders of all four species were present during both diurnal and nocturnal sampling.

**Characteristics of the Web.** The four spider species differed in body size (Table 2; Fig. 1) and in the height

**Table 2.** Results of ANOVA/ANCOVA models testing for differences among four species of orb-weaving spiders and two life stages in body size and characteristics of the web

Model	Dependent variable	Term	F	df	P
ANOVA	Body size	Overall	87.4	15,412	<0.001
		Life stage	73.3	1	<0.001
		Species	73.5	3	<0.001
		Year	15.7	1	<0.001
		Life stage $\times$ species $\times$ year	31.7	10	<0.001
ANCOVA	Web diameter	Overall	43.0	8,411	<0.001
		Body size of spider	46.3	1	<0.001
		Life stage	4.29	1	0.04
		Species	36.7	3	<0.001
		Life stage $\times$ species	2.61	3	0.05
ANCOVA	Height of hub above ground	Overall	14.62	16,411	<0.001
		Body size of spider	10.6	1	0.001
		Life stage	0.26	1	0.61
		Species	17.6	3	<0.001
		Year	16.0	1	0.001
ANCOVA	Spacing of mesh in webs	Life stage $\times$ species $\times$ year	8.84	10	<0.001
		Overall	24.0	5,363	<0.001
		Body size of spider	3.10	1	0.08
		Life stage	1.66	1	0.20
		Species	35.0	3	<0.001

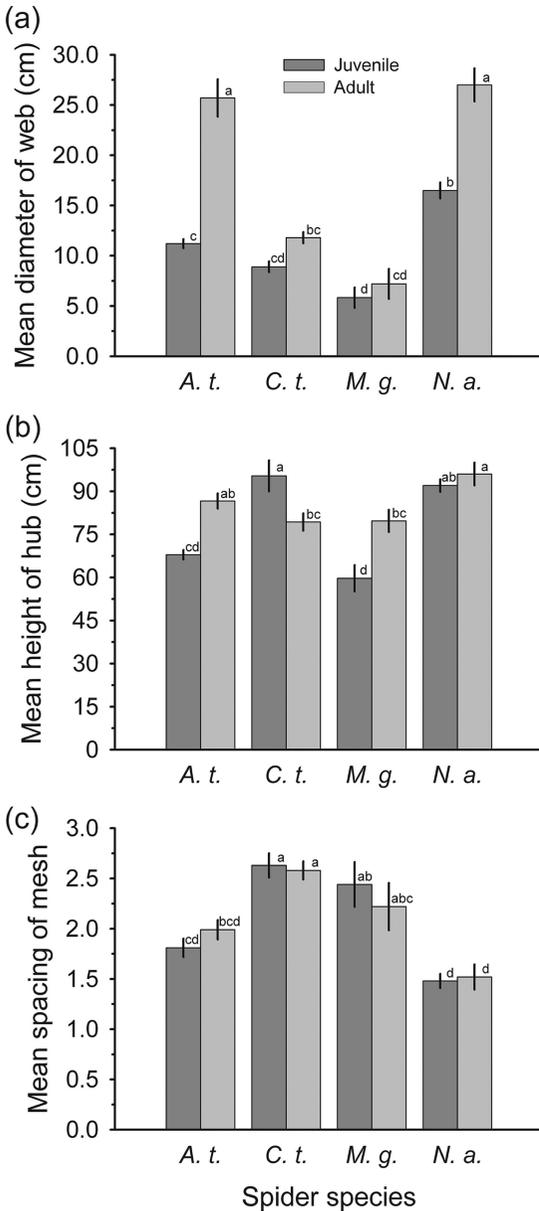


Fig. 2. Structural characteristics of webs (means  $\pm$  SE) of juveniles and adults of the orb-weaving spiders *A. trifasciata* (*A. t.*), *C. turbinata* (*C. t.*), *M. gibberosa* (*M. g.*), and *N. arabesca* (*N. a.*): (a) diameter of web; (b) height of web hub above the ground; (c) spacing of mesh within webs (1 = close, 2 = intermediate, and 3 = wide). Means with different letters are significantly different (Fisher LSD means separation test,  $P < 0.05$ ).

and structure of their webs (Table 2; Fig. 2). Life stages within species differed only in body size and web diameter (Table 2; Fig. 1). Although adult *A. trifasciata* were by far the largest spiders, being 1.8 times larger than adults of the next largest species, *N. arabesca* (Fig. 1), the webs of the two species were of similar size (Fig. 2a). Adult *N. arabesca* and juvenile *C.*

Table 3. Relative frequency [mean ( $\pm$ SE) across years] at which adult and juvenile orb-weaving spiders of four species attached their webs to different types of vegetation (see text; percentages calculated within rows)

Species and life stage	Vegetation type			
	Goldenrod	Forbs other than goldenrod	Grass	Multiple plant types
<i>Argiope trifasciata</i> adult	90.3 (9.70)	0.81 (0.81)	0.00 (0.00)	8.85 (8.85)
<i>A. trifasciata</i> juvenile	72.3 (8.70)	4.50 (2.78)	2.59 (2.59)	20.6 (8.50)
<i>Cyclosa turbinata</i> adult	60.0 (14.2)	20.2 (9.05)	0.00 (0.00)	19.9 (5.10)
<i>C. turbinata</i> juvenile	58.8 (24.5)	34.7 (18.0)	0.00 (0.00)	6.60 (6.60)
<i>Mangora gibberosa</i> adult	83.4 (16.7)	2.78 (2.78)	0.00 (0.00)	13.9 (13.9)
<i>M. gibberosa</i> juvenile	71.2 (21.2)	3.85 (3.85)	8.35 (8.35)	16.7 (16.7)
<i>Neoscona arabesca</i> adult	62.5 (12.5)	10.1 (6.57)	0.00 (0.00)	27.4 (5.95)
<i>N. arabesca</i> juvenile	58.3 (16.8)	14.2 (10.3)	1.91 (0.02)	25.7 (6.45)

*turbinata* built their webs higher above the ground than spiders of other species (Fig. 2b). Webs of juvenile and adult *N. arabesca* were relatively close-meshed compared with other species, whereas those of juvenile and adult *C. turbinata* had the widest mesh (Fig. 2c). Juvenile *M. gibberosa* were smaller spiders that spun small and relatively wide-meshed webs that were closer to the ground (Figs. 1 and 2a-c).

Spiders usually attached their webs to goldenrod plants (Table 3). Nevertheless, the spider species and life stages differed in the frequency with which they used the four types of vegetation for attachment of webs (contingency test;  $\chi^2 = 151.2$ ,  $df = 21$ ,  $P < 0.001$ ). For example, adult *M. gibberosa* attached webs more often to goldenrods and less often to other types of vegetation than juveniles of the same species ( $\chi^2 = 9.37$ ,  $df = 3$ ,  $P = 0.025$ ). Adult and juvenile *C. turbinata* differed most dramatically from other species in their choice of plants for attaching webs, more often using forbs other than goldenrod, such as species of *Ambrosia* (ragweed), *Asclepias* (milkweed), and *Cirsium* (thistle; Table 3).

**Prey Captured by Spiders.** We identified 277 arthropods that had been collected from spider webs, most being in the suborder Homoptera (primarily Cicadellidae, Cercopidae, Delphacidae, Aphididae, Membracidae), but others in the orders Diptera (primarily Cecidomyiidae, Chironomidae, Drosophilidae), Hymenoptera (primarily unidentified parasitoids, Formicidae), Hemiptera (other than Homoptera; primarily Miridae), Coleoptera (primarily Chrysomelidae, Coccinellidae), Thysanoptera (primarily Thripidae), and Lepidoptera (all Heterocera; Table 4). Spider species and life stages differed in the frequency with which they captured the different types of prey (contingency test  $\chi^2 = 340.0$ ,  $df = 30$ ,  $P < 0.001$ ). For example, juvenile *A. trifasciata* and *N. arabesca* most frequently captured homopteran prey (primarily Cicadellidae), whereas ju-

**Table 4.** Total abundance (with relative mean frequency  $\pm$  SE, across years) of different types of prey collected from webs of juvenile and adult female orb-weaving spiders of three species (percentages calculated within rows)

Spider species and life stage	Taxon of prey (suborder or order)						
	Hemiptera	Homoptera	Thysanoptera	Coleoptera	Lepidoptera	Diptera	Hymenoptera
<i>A. trifasciata</i> adult	4 (11.8 $\pm$ 11.8)	0	0	6 (39.7 $\pm$ 10.3)	2 (5.9 $\pm$ 5.9)	5 (14.7 $\pm$ 14.7)	2 (27.9 $\pm$ 22.1)
<i>A. trifasciata</i> juvenile	2 (5.0 $\pm$ 5.0)	17 (45.3 $\pm$ 10.3)	5 (13.1 $\pm$ 2.0)	2 (5.3 $\pm$ 0.28)	0	7 (18.6 $\pm$ 3.6)	5 (12.8 $\pm$ 7.2)
<i>C. turbinata</i> adult	3 (8.9 $\pm$ 4.4)	19 (50.6 $\pm$ 3.9)	2 (5.6 $\pm$ 1.1)	2 (5.6 $\pm$ 1.1)	0	5 (14.6 $\pm$ 5.5)	6 (14.7 $\pm$ 8.0)
<i>C. turbinata</i> juvenile	3 (3.4 $\pm$ 3.4)	6 (28.9 $\pm$ 26.7)	2 (6.7 $\pm$ 4.4)	1 (1.1 $\pm$ 1.1)	0	27 (35.1 $\pm$ 24.0)	14 (24.8 $\pm$ 2.6)
<i>N. arabesca</i> adult	1 (3.3 $\pm$ 3.3)	2 (13.3 $\pm$ 6.7)	0	1 (10.0 $\pm$ 10.0)	2 (6.7 $\pm$ 6.7)	14 (66.7 $\pm$ 6.7)	0
<i>N. arabesca</i> juvenile	6 (6.1 $\pm$ 1.2)	52 (55.1 $\pm$ 6.0)	1 (0.91 $\pm$ 0.91)	6 (5.8 $\pm$ 3.3)	6 (5.6 $\pm$ 5.6)	23 (25.0 $\pm$ 6.8)	2 (1.8 $\pm$ 1.8)
Total	19 (6.4 $\pm$ 1.4)	96 (32.2 $\pm$ 9.0)	10 (4.4 $\pm$ 2.1)	18 (11.3 $\pm$ 5.8)	10 (3.0 $\pm$ 1.4)	81 (29.1 $\pm$ 8.2)	29 (13.7 $\pm$ 4.7)

venile *C. turbinata* most frequently captured dipteran prey (primarily Chironomidae). The size of prey that were captured in webs was strongly correlated with the body size of the spider but not spider species or life stage (overall ANOVA,  $F_{5,107} = 11.0, P < 0.001$ ; body size of spider,  $F_1 = 25.4, P < 0.001$ ; spider life stage,  $F_1 = 0.02, P = 0.89$ ; spider species,  $F_3 = 0.02, P = 1.0$ ).

By vacuum sampling vegetation within study plots, we collected a total of 9,573 insects, most of which were in the same families as were prey that we had removed from spider webs (see above). The suborder Homoptera was again dominant ( $37.3 \pm 3.0\%$  of total), followed by the Diptera ( $26.0 \pm 0.5\%$ ), Hemiptera ( $15.8 \pm 1.4\%$ ), Hymenoptera ( $11.9 \pm 2.9\%$ ), Coleoptera ( $4.62 \pm 2.1\%$ ), Thysanoptera ( $3.66 \pm 1.4\%$ ), and Lepidoptera ( $0.46 \pm 0.3\%$ ). The spider community considered as a whole, and adult *C. turbinata* specifically, captured prey in approximately the same proportions that they occurred in the habitat ( $\chi^2$  contingency test = 8.14,  $df = 6, P = 0.23$ ;  $\chi^2 = 7.94, df = 5, P = 0.16$ , respectively), but that was not true for adults of the remaining species or juveniles of any species ( $P < 0.05$ ).

The number of homopterans and dipterans captured per individual spider was not influenced by the body size of the spider or any characteristics of the web (AIC<sub>c</sub> model  $R^2$  values  $< 0.05$ ). Body size of prey in general was positively associated with body size of spiders (regression coefficient  $\pm$  SE =  $2.15 \pm 0.30$ ) in the best model ( $\Delta AIC_c = 0.0, \Sigma w_i = 0.31, adj. R^2 = 0.35$ ; Table 5). However, six models that relate spider and web characteristics with the size of prey have reasonable support ( $\Delta AIC_c < 4$ ), so we calculated the relative importance of each predictor variable by summing the Akaike weights

for each model in which each predictor variable appeared (Anderson 2008). Body size of the spider was the most important predictor variable because it is included in every model that carries weight ( $\Sigma w_i = 1.0$ ). The diameter of webs, the height of the hub above the ground, and the spacing of mesh within webs seem to be uninformative variables with respect to prey size ( $\Sigma w_i = 0.29$ ;  $\Sigma w_i = 0.26$ ;  $\Sigma w_i = 0.39$ , respectively), as also indicated by the lack of an improvement in the log-likelihood of models when these variables are included (Anderson 2008).

**Discussion**

The spider species, and even life stages, differed in the size, structure, and position of their webs and the types of plants to which they were attached. Consistent with this variation in web characteristics, the species also differed in the types of prey that they captured, supporting our hypothesis that they would partition the available prey. Juveniles and adults of the same species also differed in prey type. Nevertheless, the community of orb-weaving spiders at our study sites, taken as a whole, captured prey in approximately the same relative proportions that they occur in the habitat, which suggests that the various and diverse type of prey were equally likely to be captured. All of the spider species maintained a generalist diet, consistent with other species of orb-weaving spiders (Nyffeler and Benz 1989, Ludy 2007).

The size of prey that spiders captured was associated with body size of spiders, with large spiders capturing larger prey, as has been reported for other spider species (Enders 1974, Brown 1981, Castillo and Eberhard 1983, Murakami 1983). However, we were not able to determine which qualities of webs were responsible for this relationship. Perhaps webs of larger spiders had thicker silk threads or greater amounts of adhesive compounds, which we did not consider in our study, and so were better able to capture larger prey that could extract themselves from weaker webs. We also found no relationship between the type of prey captured and any attribute of spiders or their webs. However, our source of data (dead prey in webs) may have been inadequate to test these relationships because spiders of many species remove dead prey from their webs after feeding on them (Turnbull 1973, Olive 1980).

**Table 5.** Best fit AIC<sub>c</sub> models for body size of prey (the dependent variable) with explanatory variables body size of spider and web structure

Explanatory variables	K	log (L)	$\Delta AIC_c$	$w_i$	adj. $R^2$
Body size	3	-99.0	0	0.31	0.35
Body size, web diameter	4	-98.6	1.2	0.17	0.35
Body size, web height	4	-98.8	1.6	0.14	0.35
Body size, mesh spacing	4	-98.4	1.0	0.18	0.35
Body size, web diameter, mesh spacing	5	-98.2	2.6	0.08	0.35
Body size, web height, mesh spacing	5	-98.2	2.6	0.08	0.35

K = no. of parameters in the model.

### Acknowledgments

We thank E. Pardungkiattisak, J. Hitchens, D. Rahe, A. Richardson, M. Currier, P. Masonick, R. Mitchell, P. Reagel, and S. Yi for technical assistance in the field. We thank D. R. Horton and two anonymous reviewers for constructive comments on a draft of the manuscript. We also thank J. Coddington and J. Spagna for assistance with spider identification, S. Buck for maintenance of the research plots, and C. Cáceres for the use of analytical equipment. Partial financial support was provided by a Summer Research Grant from the Program in Ecology, Evolution, and Conservation Biology awarded to M.L.R. This research was in partial fulfillment of a PhD degree for M.L.R. from the University of Illinois at Urbana-Champaign.

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Received 3 January 2009; accepted 23 March 2009.