

Habitat selection in a large orb-weaving spider: vegetational complexity determines site selection and distribution

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Abstract. 1. The distribution of the large orb-weaving spider *Argiope trifasciata* in old field habitats of North America and the habitat selection process this species used was studied for 2 years.

2. Because web spiders have limited dispersal abilities and an energetically costly prey capture device, they do not have the ability to sample potential foraging sites. Structural complexity of the vegetation to which the web must be attached is relatively easy to assess. The hypothesis that the structural complexity is a primary factor in determining initial web site selection was tested both by relating the natural distribution of the spiders across habitats to vegetational complexity and by manipulating the complexity of the habitats in a series of experiments.

3. *Argiope trifasciata* was not distributed evenly among three old field vegetation types. Habitat complexity was related to spider density in both years although no measure of insect activity, prey capture, or prey consumption was correlated with spider distribution.

4. Three experimental manipulations were conducted to test the impact of habitat structure on spider establishment: (1) the amount of natural vegetation was reduced, (2) structures were added to a simple habitat, and (3) the complexity of the structures added was varied. In each case, spiders were introduced and establishment of webs was monitored. In all manipulations, spider establishment was related to the complexity of the substrate available.

5. These results are important for understanding the cues that influence foraging site selection and therefore provide insight into the distribution of species with limited dispersal abilities and high site investment requirements.

Key words. *Argiope trifasciata*, distributional limitations, foraging decisions, habitat selection, habitat structure, orb-web spiders, spatial heterogeneity.

Introduction

The ability to distinguish and select among habitats is one of the most evolutionarily significant traits possessed by an organism as it determines the selective environment encountered by individuals (Jaenike & Holt, 1991; Pulliam, 1996). The structural complexity of the environment is clearly related to both the abundance and diversity of species in an area as well as the behaviour of the organisms inhabiting it (MacArthur & MacArthur, 1961; Hart & Horwitz, 1991;

Uetz, 1991; Crist *et al.*, 1992; Cartar & Real, 1997). Complexity is relatively easy for an animal to assess and it may be correlated with other habitat features such as foraging sites, retreats, or nesting sites, which are much more difficult to assess. Increased vegetational complexity may also be an indicator of the microhabitat features available and of the abundance of resources, potential predators, and/or competitors in the habitat (Andow, 1991; Heck & Crowder, 1991; Uetz, 1991).

Many studies have demonstrated that there are clear associations between spider abundance and diversity and the structural diversity of the habitat (e.g. Lowrie, 1948; Barnes, 1953; Robinson, 1981; Greenstone, 1984; Rypstra, 1986; Herberstein, 1997; Dennis *et al.*, 1998; Halaj *et al.*, 1998).

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Even though a strong case can be made for this association, recent reviews have concluded that more experimentation is critical to tease out the specific aspects of the environment to which the spiders are responding (Uetz, 1991; Wise, 1993; Rypstra *et al.*, 1999). The high cost of web construction coupled with the low dispersal capabilities of web spiders limits their ability to sample different localities as they search for an optimal foraging site (Janetos, 1986; Vollrath, 1987). Nevertheless, a bad decision usually has direct fitness ramifications because egg production is frequently correlated with recent prey consumption (Vollrath, 1987; Ward & Lubin, 1993; Wise, 1993). Because spiders are the dominant invertebrate predator in most terrestrial ecosystems (Wise, 1993), an understanding of the features that influence their distribution is important for understanding food webs and maximising their potential as agents of biological control (Riechert & Lockley, 1984; Riechert & Bishop, 1990; Rypstra *et al.*, 1999).

In the work reported here, the hypothesis that the structural complexity of the environment is the primary determinant of web site selection in the spider species *Argiope trifasciata* (Forsk. 1775) (Araneae; Araneidae) was tested. In previous work with this species and its congeners, both habitat complexity and prey abundance were found to be related to its distribution across habitat types and affected web site residence times (Olive, 1981, 1982; Bradley, 1993; McNett & Rypstra, 1997) but those results were not without ambiguity (Enders, 1976, 1977; Horton & Wise, 1983). More specifically, the aspects of initial web site acceptability as they might relate to distribution across habitats have not been tested. This species was selected because: (1) females are large (15–25 mm in length at maturity) and therefore easy to monitor in a natural setting; (2) they are very abundant in SW Ohio, with densities as high as 0.82 m⁻² at Miami University's Ecology Research Center; (3) they build a large, energetically costly web, so the web site selection should be important to their energy budget (Enders, 1976, 1977; Olive, 1981); and (4) they are common predators in gardens and agroecosystems (Kaston, 1948; Levi, 1968), so understanding the details of their distribution may be important for biological control.

Materials and methods

Censuses of local habitats

In 1993, *A. trifasciata* was surveyed in a 244-m² area at Miami University's Ecology Research Center, Ohio, U.S.A. This area encompassed three vegetation types that comprise old field habitats in which this species is commonly found (Kaston, 1948; Levi, 1968). Approximately 170 m² of the area was dominated by thistle *Cirsium arvense*, 24 m² by goldenrod *Solidago canadensis* and *S. graminifolia*, and 50 m² by grasses *Elymus* sp., *Festuca* sp., and *Phleum* sp. All the vegetation in the area was searched visually for *A. trifasciata* on 17 September 1993. When a female was found, its location within the area was mapped and the predominant vegetation type to which its web was attached (minimally more than 70% of attachment points) was recorded. The number of prey in the web was counted.

Total body length and abdomen width were measured to the nearest 0.1 mm. Because of the large size of these spiders, it was possible to take these measurements with dial calipers without disturbing the spider. The abdomen expands as the spider feeds, so these measurements provide an indication of recent prey consumption by the spiders (McNett & Rypstra, 1997). Web location, prey in the webs, and body size were monitored weekly until 22 October when a hard frost killed those spiders still alive. The distribution of spiders in relation to the distribution of vegetation types was tested using the χ^2 test. Mean spider body size and mean prey capture in each vegetation type across all censuses were compared using one-way ANOVAS.

In order to quantify vegetational complexity, the area was divided into 10 equal-area subplots. In each subplot, a metre stick was held upright at six locales determined by random number generator and all pieces of vegetation contacting the metre stick were counted. Too few vegetation samples were taken from the grass and no spiders were found in the goldenrod areas so these data were excluded from further analysis. The number of spiders in each subplot in the thistle area was regressed on the number of vegetational contacts (a measure of web attachment sites).

In 1994, female *A. trifasciata* in nine 5 × 5 m plots were censused. Three of the plots were located randomly in each of three vegetation types: thistle, grass, and goldenrod. The plots were spaced at least 4 m apart to eliminate movement of spiders from one to another during the season. This distance was chosen because, in other studies, adult spiders were not observed to move more than 2 m from a previous web site (McNett, 1995). *Argiope trifasciata* were censused weekly from 9 August to 12 November 1994, after which no spiders remained. The location of each spider was recorded. Total length and abdomen width of each individual were measured to the nearest 0.1 mm using dial calipers. The number and length (to the nearest 0.1 mm) of any prey captured in the web were also recorded. The season was divided into four time periods. Time 1 included censuses on 9 August, 24 August, and 2 September. Time 2 included censuses on 9 September, 16–17 September, and 23 September. Time 3 included censuses on 1 October, 8 October, and 14 October. Time 4 included censuses on 22 October, 30 October, 5 November, and 12 November. Data for each of the censuses within each time period were averaged. Spider distribution across habitats was analysed for the second time period using a χ^2 test. This time was selected because it was most comparable to the census conducted in 1993. Mean body measurements of spiders and the size and number of insects found in the webs in different habitats within each time period were compared using one-way ANOVAS.

Sticky traps were used as an additional measure of prey availability in all three vegetation types. Each trap consisted of a 20 × 20 cm colourless piece of plastic to which a layer of Tangle TrapTM (Tangle Foot, Grand Rapids, Michigan) adhesive was applied. Each month from August to November, nine 400-cm² traps were hung in each of the nine plots at locations determined by randomly generated coordinates within a 25-m² grid. Traps were suspended from plants or metal reinforcing rods. Trap height was determined randomly within the range of 15 and 92 cm, which was the range of

heights at which webs were located in 1993. Trap orientation (N, S, E, W) was determined randomly. Traps were set between 08.00 and 10.00 hours and retrieved 24 h later. The arthropods collected were counted and measured to the nearest 0.1 mm. Separate one-way ANOVAS for each of the insect census periods were used to test for differences in insect size and abundance among habitats. Linear regression was used to determine whether spider abundance was correlated with mean prey capture across plots.

On 9 September 1994, vegetational complexity was characterised at five randomly generated locations in each plot. At each location, two metre sticks were placed perpendicular to the ground 1 m apart. In order to obtain a measure of horizontal complexity, a third metre stick was placed horizontally between the other two at a height determined by a random number between 8 and 58 cm and the plant parts that contacted it were counted. This stick was repositioned to a height determined by a random number between 59 and 100 cm, and all the plant parts contacting it were counted again. The grand total of all vegetational contacts was used as a measure of potential web attachment points. Spider abundance during the same period (time 2) was regressed on this measure.

Treatment of the spiders used in experiments

In a series of experiments, the relative propensity of female *A. trifasciata* to build a web at a selected site was tested. All spiders used in manipulations were collected at Miami University's Ecology Research Center at least 100 m from census or experimental areas. The spiders were held in the laboratory at 15 °C in 1-cm diameter vials for 48 h. This temperature is below that at which the spiders are active but well above that which might cause mortality. The vials were not large enough to allow web construction and therefore minimised any changes in spider condition or hunger level. Spider selection was randomised for all experiments.

Experiment 1: manipulation of natural vegetation

In August 1994, 15 1 × 3 m plots were established at randomly determined locations in the thistle habitat where *A. trifasciata* was most abundant in 1993. Each plot was located at least 4 m from any other plot. In five plots, one-third of the thistle plants were removed. In another five plots, two-thirds of the thistle plants were removed. The remaining five plots served as controls. On 16 September 1994, all naturally occurring *A. trifasciata* individuals were removed from the plots. On 28 September, four female *A. trifasciata* were added to each plot. These spiders were counted daily until 15 October. Spider number per plot was averaged over time.

Experiment 2: addition of artificial structures

In August 1994, 10 2 × 2 m plots were established in a habitat dominated by grass 80 cm tall and another 10 plots

were located where the grass had been mowed to 5 cm. All plots were separated by at least 4 m to reduce movement of spiders from one plot to another. Two artificial structures were added to five of the plots in each of the grass subhabitats to increase the structural complexity. The other five plots in each subhabitat served as controls. The structures consisted of a 60-cm stake (2 × 3 cm) with three shrub branches, each of which bifurcated approximately 20 cm from the base (1 cm diameter, 50 cm long) glued into holes located 2–6 cm from its top. Two of these units were situated in the centre of each experimental plot and 1 m apart such that a branch of one was within 20 cm of a branch of the other. On 16 September 1994, all naturally occurring *A. trifasciata* were removed from all plots. On 28 September 1994, six female *A. trifasciata* were introduced to each plot. Plots were censused daily until 15 October 1994. Spider number per plot was averaged over time.

Experiment 3: varying complexity of artificial structures

In a final test of the response of *A. trifasciata* to habitat structure, the artificial structures were modified by making them either simpler (providing fewer potential web attachment sites) or more complex (providing more potential web attachment sites). Simple structures were similar to those described above but they had only two straight branches (1 cm diameter, 50 cm long) glued to the main stake. Complex structures were the same as those described previously. Very complex structures had five bifurcating tree branches (1 cm diameter, 50 cm long) glued to the stake. Ten 5 × 5 m plots were established in tall grass habitat and 10 5 × 5 m plots were established in the mowed grass areas. One of each type of the artificial structures was added to the centre of each plot. On 14 and 15 September 1994, three female *A. trifasciata* were introduced to each structure type in each plot, making a total of six spiders per structure type and 18 per plot. The spiders with webs attached to each structure type were counted daily until 23 September 1994. The proportion of web anchor points that was attached to the structures and the proportion attached to natural vegetation were recorded for each web.

Statistical analysis

The number of spiders in each treatment group for each experiment was averaged over time for analysis. There were insufficient replicates to determine whether the data were distributed normally; Barlett's test was used to verify the assumption of equality of variances among treatment groups. In order to analyse the proportion of web anchor points attached to the structures in expt 3, proportions were arcsin transformed before analysis (Neter *et al.*, 1985). If appropriate, data for a given experiment were compared using a one-way ANOVA and Fisher's pairwise comparisons. When no spiders established themselves in a particular treatment, those data were excluded from analysis and the *T*-test was used to compare the other two groups. Differences were considered significant when $P < 0.05$.

Table 1. Distribution of spiders across vegetation types in September 1993 and 1994. In order to calculate expected number of spiders for χ^2 analysis, the proportion of the total census area composed of one vegetation type was multiplied by the total number of spiders censused (1993: $\chi^2 = 38.60$, d.f. = 2, $P < 0.001$; 1994: $\chi^2 = 11.26$, d.f. = 2, $P < 0.01$).

Habitat type	Area in habitat (m ²)	Per cent area in habitat	Expected spider number	Number of spiders found	Spiders per m ²
1993					
Thistle	170	69.7	104.6	139.0	0.818
Grass	50	20.7	31.1	11.0	0.220
Goldenrod	24	9.6	14.3	0.0	0.000
1994					
Thistle	75	33.3	10.4	10.7	0.143
Grass	75	33.3	10.4	18.0	0.240
Goldenrod	75	33.3	10.4	2.7	0.036

Results

Habitat censuses

In 1993, *A. trifasciata* was found in higher numbers than expected in thistle, in lower numbers than expected in grass, and was absent from goldenrod ($\chi^2 = 38.6$, d.f. = 2, $P < 0.001$) (Table 1). There was no difference in prey capture between spiders in grass and those in thistle over the season (Table 2). Likewise, spiders inhabiting grass or thistle were not significantly different in either abdomen width or total body length (Table 2). The amount of vegetation that contacted the vertical metre stick was correlated positively with the number of spiders inhabiting thistle ($r^2 = 0.748$, $P < 0.001$) (Fig. 1).

Overall density of *A. trifasciata* was higher in 1993 ($1.14 \pm 0.42 \text{ m}^{-2}$) than in 1994 ($0.64 \pm 0.13 \text{ m}^{-2}$) ($F_1 = 11.75$, $P < 0.01$). *Argiope trifasciata* was not distributed evenly across vegetation types during time 2 in 1994, which was most comparable to the census time in 1993 (Table 1). The spiders were in expected numbers in thistle but were more abundant than expected in grass and, as in 1993, were scarce in goldenrod ($\chi^2 = 11.3$, d.f. = 2, $P < 0.01$).

There were no significant differences in the number or size of prey captured by spiders inhabiting the three vegetation types in 1994 (Table 2). Total body length did not differ among the habitats but spiders in the goldenrod, where the population levels were lowest, had significantly larger abdomens (Fisher pairwise comparisons, $P < 0.05$) (Table 2). In 1994, the number of prey captured and size of prey per spider increased with time until time 4 (10 October to 12 November) when there were no captures (Table 2). Measures of spider abdomen width and total body length also increased over time (Table 2).

There was no significant difference among habitats in the number of prey captured by sticky traps for any time period in 1994 (Table 3), however prey size differed among habitats during time 1 and time 2 when sticky traps in goldenrod captured the largest insects (Table 3). There was no correlation between prey abundance as estimated by the

captures on sticky traps and spider number per plot in any time period (Table 3).

In 1994, there was a significant correlation between the total amount of vegetation that contacted the metre sticks and the number of spiders inhabiting each plot across the habitats during time 2 ($r^2 = 0.713$, $P < 0.001$) (Fig. 1).

Experiment 1: manipulation of natural vegetation

The removal of thistle plants had a significant effect on spider establishment ($F_2 = 7.16$, $P < 0.01$) (Fig. 2). Spiders preferred control thistle plots over plots from which plants had been removed (Fisher, $P < 0.05$). Spider establishment did not differ between plots with one-third of the plants removed and those with two-thirds of the plants removed (Fisher, $P > 0.05$).

Experiment 2: addition of artificial structures

In the plots where the grass had been mowed, no spiders remained in either the control plots or in the plots where structures had been added, so these treatments were excluded from further analysis. In the natural grass plots, more spiders remained in the plots where units had been added than in the control plots that lacked structures ($T_1 = 30.49$, $P < 0.001$) (Fig. 3).

Experiment 3: varying complexity of artificial structures

Overall, spider establishment was low in this experiment ($< 20\%$ of spiders stayed), so data from the natural grass and mowed areas were pooled for analysis. No spider built a web on the simple structures so this treatment was excluded from further analysis. Spider establishment on the complex

Table 2. Mean \pm SE (sample size) of body size measurements and prey capture data for 1993 (one time period) and 1994 (three time periods). In 1993 there were no spiders in goldenrod and prey size data were not collected.

Year	Habitat	Time 1	Time 2	Time 3	Habitat	Time	Habitat \times time
Abdomen width (mm)							
1993	Grass		4.71 \pm 0.12 (11)		$F_1 = 0.47$		
1993	Thistle		4.41 \pm 0.32 (137)		NS		
1994	Grass	2.17 \pm 0.08 (46)	3.70 \pm 0.17 (53)	5.97 \pm 0.45 (17)	$F_2 = 6.41$	$F_2 = 61.92$	$F_4 = 3.85$
1994	Goldenrod	2.07 \pm 0.01 (22)	4.72 \pm 1.50 (8)	9.84 \pm 0.47 (4)	$P < 0.05$	$P < 0.001$	$P < 0.05$
1994	Thistle	2.08 \pm 0.10 (26)	4.01 \pm 0.04 (33)	5.81 \pm 0.68 (28)			
Body length (mm)							
1993	Grass		12.64 \pm 0.19 (11)		$F_1 = 0.39$		
1993	Thistle		13.34 \pm 0.64 (139)		NS		
1994	Grass	6.21 \pm 0.05 (46)	10.99 \pm 0.50 (53)	13.74 \pm 0.63 (17)	$F_2 = 1.03$	$F_2 = 49.08$	$F_4 = 1.06$
1994	Goldenrod	5.78 \pm 0.26 (22)	10.70 \pm 3.20 (8)	17.20 \pm 0.80 (4)	NS	$P < 0.001$	NS
1994	Thistle	5.55 \pm 0.14 (26)	11.39 \pm 0.40 (33)	13.21 \pm 1.12 (28)			
Prey capture per spider							
1993	Grass		0.36 \pm 0.15 (25)		$F_1 = 0.60$		
1993	Thistle		0.45 \pm 0.04 (427)		NS		
1994	Grass	0.10 \pm 0.02 (46)	0.25 \pm 0.02 (53)	0.19 \pm 0.10 (17)	$F_2 = 3.80$	$F_2 = 4.23$	$F_4 = 1.26$
1994	Goldenrod	0.08 \pm 0.08 (22)	0.13 \pm 0.13 (8)	0.00 \pm 0.00 (4)	NS	$P < 0.05$	NS
1994	Thistle	0.12 \pm 0.01 (26)	0.37 \pm 0.06 (33)	0.18 \pm 0.12 (28)			
Prey length (mm)							
1994	Grass	2.03 \pm 0.13 (4)	4.35 \pm 1.27 (13)	7.00 \pm 1.70 (3)	$F_2 = 0.97$	$F_2 = 8.78$	$F_4 = 1.11$
1994	Goldenrod	1.70 \pm 0.00 (1)	4.00 \pm 0.00 (1)	No data	NS	$P < 0.05$	NS
1994	Thistle	2.77 \pm 0.72 (3)	5.53 \pm 1.57 (12)	11.24 \pm 2.91 (10)			

structures (three branches) was significantly lower than establishment on the very complex structures (five branches) ($T_1 = 6.66$, $P < 0.05$) (Fig. 4).

The webs built in the natural grass were less dependent on the artificial structures for web support than were webs built where the grass had been mowed ($T_1 = 243.6$, $P < 0.01$). In the mowed habitat, $87.75 \pm 12.25\%$ of the support threads were attached to the structures, whereas in the natural grass habitat only $20.00 \pm 2.39\%$ were attached to the structures. Spiders attached a greater proportion of their support threads to the very complex structures ($56.9 \pm 15.4\%$) than they did to the complex structures ($22.2 \pm 6.1\%$) ($T_1 = 66.4$, $P < 0.001$).

Discussion

The propensity of *A. trifasciata* to build a web at a particular site is clearly related to vegetational complexity. Natural spider abundance correlated with the measure of web attachment points or structural complexity in both years of the study. Likewise, in all the habitat manipulations, spider establishment was related to the available substrate, regardless of whether natural vegetation was altered or artificial structures were provided. Even though there were some differences in prey consumption by spiders (as evidenced by abdomen size), they were never correlated with spider abundance. In fact, spiders in the least preferred habitat (goldenrod) had the largest abdomens and abdomen size is the morphological character most greatly influenced by recent prey consumption (McNett & Rypstra, 1997). If the spiders were tracking prey availability,

spider density should have been highest in goldenrod. These results suggest that the structure of the vegetation is the primary factor in the selection of a new web site.

These results suggest a fairly simple scenario to explain the habitat distribution of this large web-building spider. Structural features of the environment determine initial site selection, but how long the spiders remain at that site will depend on their foraging success there. Studies have demonstrated that residence time is related to disturbance or web destruction (which may occur in more open sites) (Enders, 1976; Hodge, 1987), microhabitat features such as temperature or humidity (Biere & Uetz, 1981), growth of the spider and a commensurate change in the structural requirements for web construction (Lubin *et al.*, 1993), and/or prey capture success (Bradley, 1993; Miyashita, 1994; McNett & Rypstra, 1997). A spider cannot assess these parameters accurately without sampling and, with the high energetic costs associated with web construction, sampling is expensive. The reason why habitat complexity is correlated with spider abundance across the landscape is due to a combination of minimally acceptable prey capture rates and the limited dispersal ability of the spiders. Once a spider has selected a site, it moves only when prey capture is below some threshold and, because it cannot easily move great distances, it tends to remain in the same subhabitat.

Spiders in the preferred vegetation types were at a high density so exploitative competition may have reduced their prey capture rates, however all measures of prey capture (actual captures, abdomen size, and sticky traps) suggest that there were few real differences in the activity of potential prey

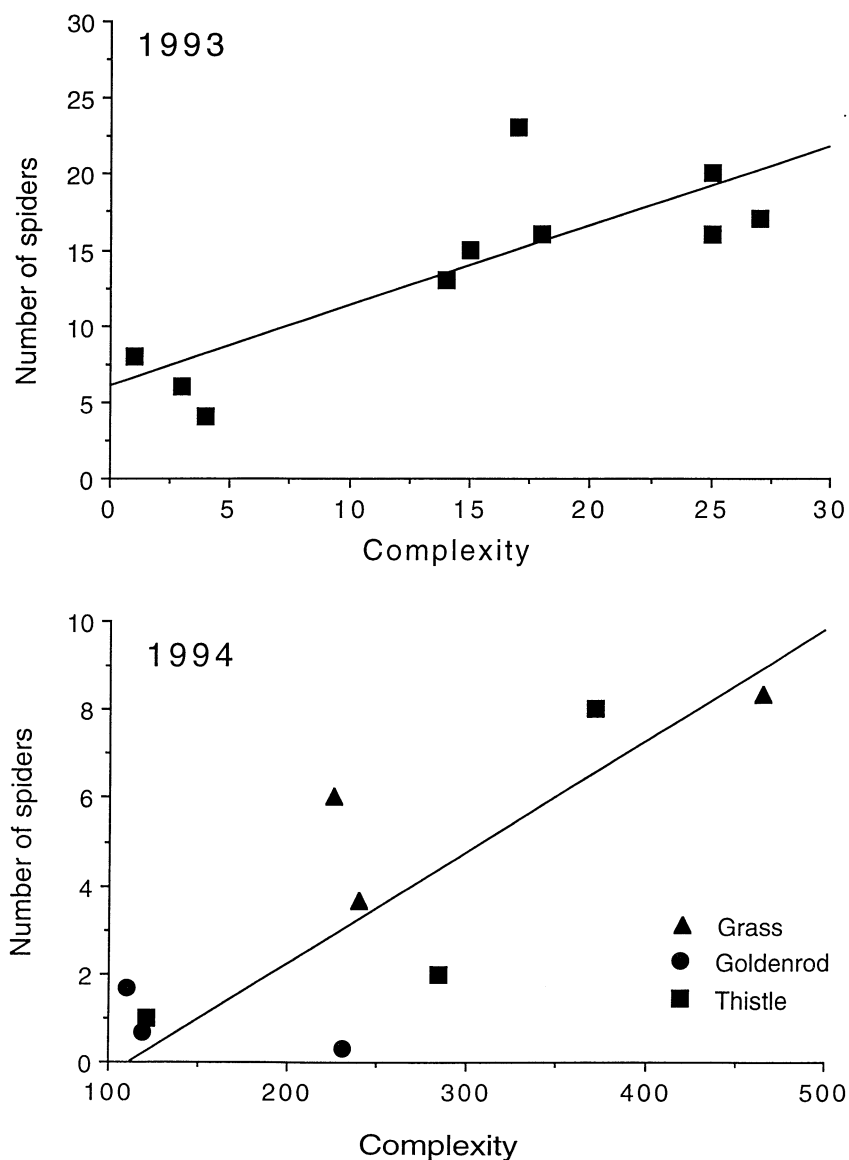


Fig. 1. Relationship between the number of spiders and vegetation complexity for 1993 ($r^2=0.748$, d.f.=1, $P<0.001$) and 1994 ($r^2=0.748$, d.f.=1, $P<0.001$). The data used in this analysis were from September of both years. The specific measure of vegetation complexity was different in each year (see text for full explanation).

among the vegetation types under study (Table 2). Likewise, in all manipulations, spider densities were set at intentionally low levels so that competitive effects would be minimised and the importance of the structure available to spider establishment could be established. Similarly, Horton and Wise (1983) found that this species altered foraging, with consequent effects on growth, more in response to physical factors and vegetation structure than in response to competitive interactions.

A variety of organisms has been shown to select vegetationally complex habitats, even when foraging efficiency is reduced, especially when those complex habitats have something else to offer such as protection from predation risk (Werner *et al.*, 1985; Heck & Crowder, 1991). There is no evidence of such a trade-off influencing *A. trifasciata* in this study. As mentioned

above, there were no consistent differences in prey availability or prey capture among the three habitats under study through the season. Additionally, once the spiders established themselves in the manipulated habitats, their numbers remained constant over time, suggesting that there was no differential predation pressure on these animals across habitats or among treatments. If anything, spiders that built webs on introduced structures were more exposed than those in natural vegetation, but in all cases they tended to build their webs on the periphery of the structures where they would be most obvious to visual predators such as birds.

Temperature, humidity, and other abiotic factors have been shown to influence the abundance and distribution of spiders across habitats (Riechert & Tracy, 1979; Tolbert,

Table 3. The number (mean \pm SE) and size (mean \pm SE) of insects captured on sticky traps in each habitat during 1994. Results of one-way ANOVA are shown. Insect number was regressed on number of prey captured and r^2 values are shown.

	Time 1	Time 2	Time 3	Time 4
Grass				
Number	118.7 \pm 37.5	469.0 \pm 80.6	61.0 \pm 54.6	16.3 \pm 0.9
Size (mm)	2.2 \pm 0.1	2.1 \pm 0.1	2.4 \pm 0.2	2.5 \pm 0.3
Goldenrod				
Number	74.0 \pm 7.0	421.0 \pm 76.6	93.3 \pm 8.1	18.7 \pm 2.2
Size (mm)	2.8 \pm 0.2	2.3 \pm 0.1	2.3 \pm 0.1	2.9 \pm 0.7
Thistle				
Number	186.7 \pm 87.1	643.0 \pm 183.5	80.6 \pm 19.6	13.7 \pm 0.9
Size (mm)	2.2 \pm 0.1	2.2 \pm 0.1	2.5 \pm 0.3	3.2 \pm 0.7
Statistical analysis				
Prey number	$F_2 = 1.07$	$F_2 = 0.89$	$F_2 = 1.67$	$F_2 = 97.0$
	NS	NS	NS	NS
Regression	$r^2 = 0.00$	$r^2 = 0.30$	$r^2 = 0.49$	$r^2 = 0.10$
	NS	NS	NS	NS
Prey length	$F_2 = 7.71$	$F_2 = 31.1$	$F_2 = 2.03$	$F_2 = 0.06$
	$P < 0.001$	$P < 0.001$	NS	NS

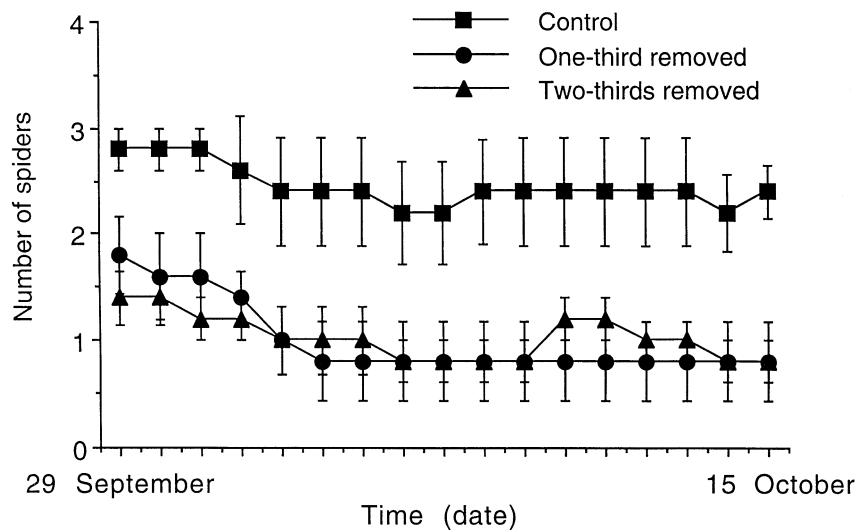


Fig. 2. The number of spiders that established webs (mean \pm SE) in the experiment in which natural thistle vegetation was manipulated. Four spiders were introduced to plots in which the density of thistle plants was reduced by one-third, two-thirds, or not at all.

1979; Wise, 1993). For example, the protection that vegetation affords from wind has been shown to be an important factor in web site tenacity for *A. trifasciata* (Enders, 1975). The use of artificial structures in these experiments controlled for the surrounding vegetation and therefore exposure to wind and other microhabitat differences. It seems unlikely that weather differences could account for the observed differences in spider establishment patterns in these manipulations or across the vegetation types these spiders inhabited in Ohio old fields.

The complexity of the structure provided to the spiders also affected the way they used the substrate for web support. Spiders attached a greater proportion of their support threads to the most complex structures than to less complex structures. Webs built in tall natural grass were less dependent on the artificial structures for web support than were webs built where the vegetation had been mowed, which was much less complex, demonstrating that habitat structure was not only a strong determinant of spider establishment but also affected how the spiders used the space available as they built their prey trap.

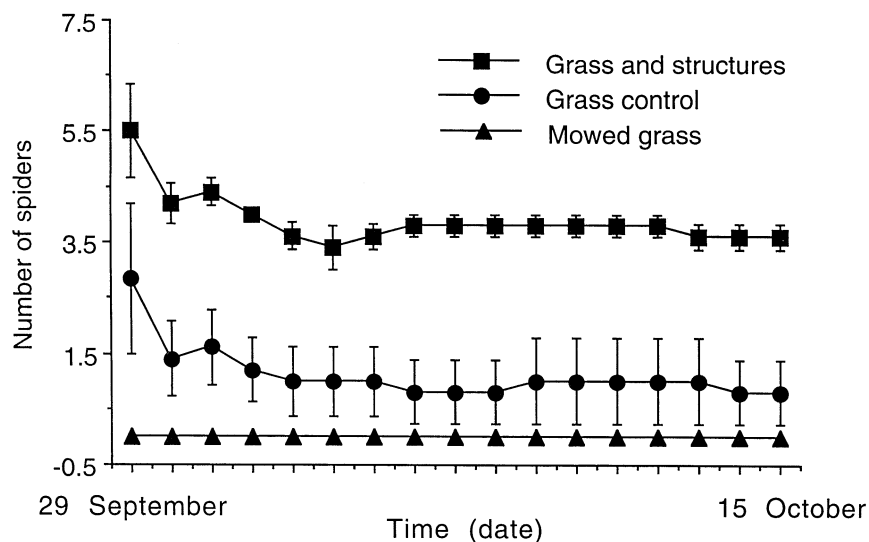


Fig. 3. The number of spiders that established webs (mean \pm SE) out of the six individuals added to grass plots with or without complex (two-branched) structures. Note that no spiders established themselves in mowed grass plots.

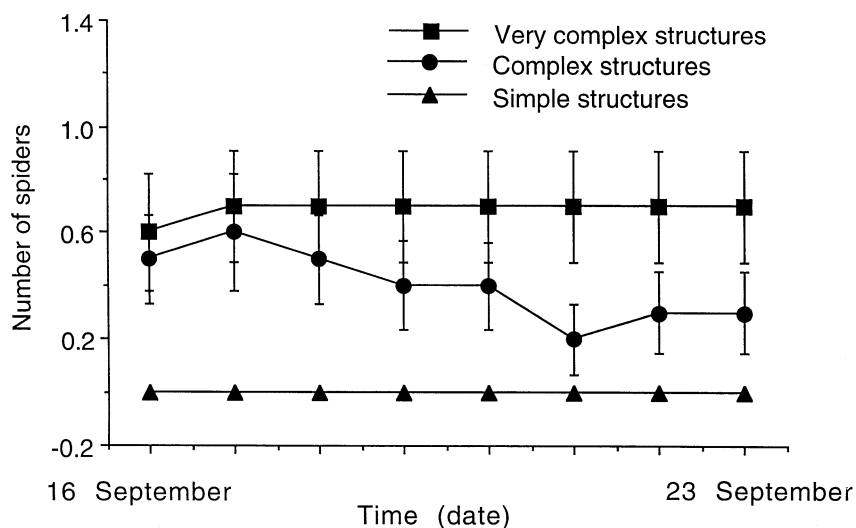


Fig. 4. The number of spiders that established webs (mean \pm SE) out of the three individuals added to simple (two-branched), complex (three-branched), and very complex (five-branched) structures. Because spider establishment was low, data from mowed and unmowed plots were pooled.

The switch in habitat preference from thistle to grass between 1993 and 1994 can be explained by the fact that the grass areas censused in the first year were considerably different from those censused in the second year. The grass areas censused in 1993 had been mowed very early in the spring and were therefore considerably shorter than the areas censused in 1994. The spring mowing probably eliminated spiders and the low numbers of spiders in this area were due to the limited dispersal ability of this species. The results of manipulations in which the natural vegetation was mowed, however, demonstrated that the lack of structure as a result of

mowing left grass habitats totally inhospitable to spider establishment.

Previous studies have shown that *A. trifasciata* can be common in goldenrod (McReynolds & Polis, 1987), yet there were very few in these goldenrod plots in either year. This distributional pattern was particularly intriguing because the few spiders found in goldenrod had wider abdomens than spiders in the other habitats, suggesting that it was a good foraging location. The absence of spiders in goldenrod could be attributed to the lower complexity of that habitat. Goldenrod had fewer total potential attachment points than the other

vegetation types and there were very few open spaces in which to place a large orb-web (Fig. 1).

Understanding the factors that result in high density and diversity of these generalist predators has important implications for biological control (Riechert & Lockley, 1984; Riechert & Bishop, 1990). In other studies, manipulations of habitat structure have resulted in food web effects attributable to increased spider densities (Riechert & Bishop, 1990; Carter & Rypstra, 1995). *Argiope trifasciata* is a common generalist predator around homes and in gardens in eastern North America (Levi, 1968). These results suggest that deliberate alterations to the structural complexity of a garden – either by altering plant placement or the addition of artificial substratum – may encourage this species and ultimately reduce pest insects.

In conclusion, *A. trifasciata* used habitat structure and the presence of available web substrate to make the decision to settle in a particular area. Because they relocate more frequently at lower prey levels (McNett & Rypstra, 1997), their final distribution across suitable habitats will reflect some combination of suitable web sites and prey capture rates above some threshold. These results may be important for understanding the distribution of a variety of species with similarly high costs of habitat sampling and low abilities to disperse and colonise new areas (Pulliam, 1996).

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