EFFECTS OF PREY SUPPLEMENTATION ON SURVIVAL AND WEB SITE TENACITY OF *ARGIOPE TRIFASCIATA* (ARANEAE, ARANEIDAE): A FIELD EXPERIMENT

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ABSTRACT. The effects of prey capture on web site tenacity and survivorship of *Argiope trifasciata* (Araneae, Araneidae) were studied in two old field habitats in southwestern Ohio. Adult females were studied in habitats dominated by grass or thistle plants. In manipulation plots, we added two crickets to the webs of approximately half the spiders. We were able to quantify differences in prey intake using morphological measurements that changed with food consumption. The spiders that did not receive supplemental food were similar in size to unmanipulated spiders in other areas that we censused. No differences were observed in survivorship or web site tenacity of spiders in grass *vs.* thistle habitats. No difference in survivorship was observed between fed spiders and those left to natural prey capture. However, spiders receiving supplemental prey relocated their webs less frequently than those spiders that were unsupplemented.

The selection of a site in which to live and forage can be a critical decision for a spider since food intake can have a substantial effect on the spider's ability to survive, grow, and ultimately reproduce (Riechert & Gillespie 1986; Vollrath 1987). The webs that spiders use as foraging tools are energetically costly (Prestwich 1977; Peakall & Witt 1976), and it is not possible for web-spiders to sample their habitat extensively before settling to forage in a particular place (Janetos 1986; Vollrath 1985, 1987). As a result, the initial selection of a site must be based on habitat features and the appropriateness of web attachment sites (Pasquet 1984; Hodge 1987a; Bradley 1993). Once the initial web is constructed, the spider acquires additional information on prey capture which can influence whether it stays or leaves.

A number of studies on a variety of species suggest that web-spiders use recent information on prey capture in deciding whether to stay or leave a particular site (Turnbull 1964; Janetos 1982; Olive 1982; Pasquet 1984; Vollrath 1985; Gillespie 1987; Rubenstein 1987; Hodge 1987b; Provencher & Riechert 1991; Bradley 1993). A variety of other factors unrelated to prey capture, such as the frequency of web destruction or damage, interactions with conspecifics, the spider's age, and/or the action of predators, can influence a spider's decision to leave or remain in a given location (Eberhard 1971; Enders 1975, 1976, 1977; Wise 1975; Pasquet 1984; Spiller 1984; Vollrath & Houston 1986; Gillespie & Caraco 1987; Craig 1987; Smallwood 1993). Clearly, if a particular population is not food limited, prey capture should not have an effect on web site tenacity (Eberhard 1971; Enders 1976; Wise 1993). However, Olive (1981) argues that the phenologies of orb-weaving spiders, particularly those in the genus *Argiope* Audouin 1827, are tied to the seasonality of insects in their environment and that they evolved under the constraints of food limitation. In enclosure experiments with *Argiope trifasciata* (Forskål 1775), he found that they abandon sites with lower rates of prey capture and aggregate in areas where he supplied prey at a higher rate (Olive 1982). A field study with *A. keyserlingi* Karsch 1881, revealed that food supplementation, even over a few days, decreased the tendency of individuals to relocate their webs (Bradley 1993). However, in experiments with *A. aurantia* Lucas 1833, prey supplementation had no effect on web site tenacity; and the likelihood of wind damage appeared to be more critical to the web relocation decision (Enders 1975, 1976).

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Olive's (1981, 1982) results influenced us to further investigate the relationship between prey capture, survivorship, and web site tenacity in *A. trifasciata*. Since the abdomen of a spider expands as it feeds (Anderson 1974; Jakob et al. 1996), we were able to quantify differences between spiders that receive supplemental prey and those left to natural prey capture without disturbing them on their webs. In this way, we were able to verify that the spiders we fed consumed the prey we provided and experienced a change in their overall body condition in some significant way as a result of prey consumption. We then tested the hypothesis that prey supplementation would increase the survivorship and web site residence time of adult females in two structurally distinct habitats.

METHODS

Study species.—*Argiope trifasciata* is a conspicuous orb-weaving spider found in gardens, tall weeds, and grasses in the eastern United States (Kaston 1948). Spiders emerge from egg sacs in May and June (Kaston 1948). Females mature in September when they are 15–25 mm in length, lay eggs in October and November, and die with the onset of winter (Scheffer 1905; Tolbert 1976). We selected this species for our investigation of the effects of prey capture on web relocation because: (1) their large size makes them easy to monitor in the field; (2) in 1993, the year before this study was conducted, we found them to be very abundant in old field habitats with densities as high as 0.82 spiders per m² (McNett 1995); and (3) although they rebuild the capture spiral of their web each day, they reuse the framework which attaches the web to the vegetation and, as a result, web relocation is costly in comparison to remaining at the same site (Enders 1976; Olive 1981).

Study site.—The study population inhabited old fields of the Miami University's Ecology Research Center, three miles north of Oxford, Butler County, Ohio, USA. Two manipulation plots (25 × 20 m) were established for prey experiments. One manipulation plot was set up in an area dominated by thistle (*Cirsium arvense*) and the second in an area dominated by grasses (*Elymus* sp., *Fustuca* sp. and *Phleum* sp.). These two habitat types were those that the spiders preferred in 1993 (McNett 1995). Three 5 × 5 m census plots

in thistle and three 5 × 5 m census plots in grass, located at least 100 m away from the manipulation plots, were used as control areas in which the spiders were counted and measured but not fed.

Prey availability.—Background prey availability was assessed in both the thistle and grass habitats using sticky traps. Each trap consisted of a 20 × 20 cm sheet of plastic to which a thin layer of Tangle Trap℠ (Tangle Foot, Grand Rapids, Michigan) was applied. Traps were suspended with string that was tied either to natural vegetation or, when necessary, to metal reinforcing rods (3.5 m in height). Trap height was randomly determined within the range of 15–92 cm. These values were selected because they corresponded to the range of heights at which webs were found in 1993 (McNett 1995). Trap orientation was determined by randomly selecting a compass direction. A total of nine 400 cm² traps were hung in each of the six census plots in the early morning of 6 October 1994 and left for 24 h. The arthropods collected were identified to order, counted and measured to the nearest 0.1 mm.

Morphological changes in the laboratory.—Twenty-two adult female *A. trifasciata* were collected and allowed to establish webs in acrylic plastic (Plexiglas℠) cages measuring 45 × 45 × 7.5 cm in the laboratory. The total body length and abdomen width of all the spiders were measured after web construction. We selected these measures because it was possible to take them without disturbing the spider in its web. After measurement, nine spiders were fed one cricket (*Acheta domestica;* approximately 150 mg in weight). All of the spiders were then left for 24 h during which time each individual replaced its capture spiral once. At that time, all of the spiders were measured again to determine if morphological differences as a result of feeding would be detectable.

During the course of two years of study of this species we were able to obtain morphological measurements in the laboratory of six females before and after eggsac deposition. Spiders were measured and left for 24 h. At that time the egg sac was noted and the spider remeasured. None of these spiders were fed between measurements.

Prey manipulation.—On 26–27 September 1994, 80 adult female *A. trifasciata* were

collected from areas at least 100 m outside the plots and individually marked on their abdomens with non-toxic paint. Spiders were held in the laboratory at 15 °C in vials 1 cm in diameter which were not large enough to allow web construction and therefore minimized any changes in their condition or hunger level. On 28–29 September 1994, all naturally occurring *A. trifasciata* from each of the two 25 × 20 m manipulation plots were removed. In the early morning of 30 September 1994, we introduced 40 randomly-chosen marked spiders to each plot by placing them on vegetation approximately 2 m away from other individuals. The next day, we searched the plots and marked the location of each spider's web by tying flagging to the vegetation near the web. There was a low establishment rate of marked spiders, so all unmarked spiders that moved into the plots after that date were assigned to a treatment group and included in further data collection. In comprehensive surveys conducted in 1993, we discovered that individuals never moved more than two meters (McNett 1995), so we were confident in our ability to follow and monitor web site changes of unmarked spiders that moved into our manipulation plots.

Introduced as well as unmarked individuals that established in the manipulation plots, were assigned randomly to one of two treatments: one group received supplemental prey and the other group was left to natural prey capture. Supplemented spiders received two adult crickets (*Acheata domestica;* approximately 300 mg) every other day in addition to the prey they captured naturally. Spiders received supplemental prey until they could no longer be located, at which time they were presumed dead. A total of 26 spiders was monitored in the thistle plot, 12 of which were fed crickets, and 30 spiders were monitored in the grass plot, 14 of which were provided with crickets.

Spider location was monitored daily from 1 October until no spiders could be found on 27 October 1994. If a spider was not found where it had been the previous day, the surrounding 60 m² area was visually searched. We were able to identify unmarked individuals by a combination of web location and abdominal patterns. Since we never observed a spider move more than 2 m from a previous web site, this large search area eliminated the

likelihood that a spider would be falsely assumed dead. If we found the spider, we recorded its new location but, if we were unable to find it, we assumed it was dead.

We measured abdomen width and total body length of all spiders in the manipulation plots to the nearest 0.1 mm on 4, 8 and 16 census days after the prey supplementation commenced. On those same dates, we counted and measured all of the spiders in our six census plots.

Statistical analysis.—The number and size of insects captured on sticky traps in grass and thistle were compared with a one-way ANOVA. The change in body size of laboratory spiders was compared using the *t*-test. The number of spiders in grass and thistle census plots over the course of the study were compared using a repeated measures ANOVA. We compared the abdomen width and body length of field measured spiders in three treatments (supplemented, unsupplemented and censused) in two habitat types (grass and thistle) using an two-way factorial ANOVA and then differences among the specific treatments were compared using Fisher Pairwise Comparisons. These three groups were compared 4, 8, and 16 census days after the prey supplementation was begun. Fed spiders on day 4 would have received prey twice (a total of four crickets), on day 8 they would have received prey four times (eight crickets), and on day 16 they would have received prey eight times (16 crickets).

In order to determine the impact of supplemental prey on survivorship, the total number of days over which we were able to locate fed and unfed spiders in the two habitats was compared using a two-way factorial ANOVA. In order to determine the impact of prey supplementation on web relocations, we also used the two-way factorial ANOVA to compare the movement frequency of fed and unfed spiders in the grass and thistle habitats.

RESULTS

Spider abundances.—There was no difference between the number of spiders inhabiting thistle or grass in the census plots (Repeated measure ANOVA, $F = 1.2$, $P = 0.3$) (Table 1). Census plots had more spiders than we were able to establish in our manipulation plots ($F = 18.96$, $P = 0.032$) (Table 1). Since densities in manipulation plots were low com-

Table 1.—Number of spiders (mean ± standard error) per square meter in old field habitats dominated by grass or thistle. In a two-way ANOVA, there were no differences between densities in grass and thistle habitats ($F = 1.2$, $P = 0.3$) but densities in manipulation plots were significantly lower than densities in census plots ($F = 18.9$, $P = 0.03$).

Plot type	Grass	Thistle
Census	0.52 ± 0.25	0.39 ± 0.12
Manipulation	0.06 ± 0.02	0.05 ± 0.02

pared to natural densities, we believe we successfully eliminated density as a potentially confounding factor in our study of the effects of habitat type and prey capture on web relocation.

Prey abundance.—Sticky traps in grass captured 60.0 ± 10.1 insects in 24 h which was not significantly different from 80.7 ± 20.2 insects captured by these traps in thistle (One-way ANOVA, $F = 0.21$, $P = 0.4$). The mean size of the insects captured by sticky traps in grass (2.39 ± 0.19 mm) was also very similar to the mean size captured in thistle (2.46 ± 0.22) ($F = 0.07$, $P = 0.7$). The insect orders Diptera and Hymenoptera made up more than 90% of the captures in both habitats.

Morphological changes.—In the laboratory, the consumption of one cricket was enough to increase total body length by 0.42 ± 0.16 mm, whereas unfed individuals shrank by 0.21 ± 0.16 mm in 24 h ($t = 7.35$, $P = 0.0005$) (Table 2). Likewise, the abdomen width of fed spiders increased by 1.34 ± 0.11 mm while the abdomen width of unfed individuals decreased by 0.22 ± 0.15 mm in 24 h ($t = 60.70$, $P < 0.0001$) (Table 2). These differences verify that these measurements are an indicator of recent feeding history and spider condition. The deposition of an eggsac re-

duced both spider abdomen width ($t = 8.2$, $P = 0.0004$) and total body length ($t = 7.9$; $P = 0.0005$) in the laboratory (Table 2). In addition, the spider's abdomen appeared shrunken and wrinkled after eggs were laid.

Prey manipulation.—Although the spiders increased in size over the course of the experiment, there were no significant differences observed between spiders inhabiting grass or thistle in the amount that either total body length (Two-way factorial ANOVA, $F = 1.34$, $P = 0.26$) or abdomen width ($F = 0.24$, $P = 0.63$) changed during the course of the study (Table 3). Unsupplemented spiders within our manipulation plots were not different in either measure of size from the control spiders in the census plots 4, 8 and 16 days after the food supplementation was begun (Fisher pairwise comparisons, $P > 0.05$) (Fig. 1). However, spiders that received supplemental prey had wider abdomens than spiders in the other two groups (unsupplemented and censused) on all three dates tested (Fisher pairwise comparisons, $P < 0.05$) (Fig. 1). Likewise, spiders receiving additional prey were longer than unsupplemented spiders in manipulation plots on all of those same dates and were longer than undisturbed spiders in the census plots on day eight. (Fisher pairwise comparisons, $P < 0.05$) (Fig. 1).

We were able to find fed spiders for 13.6 ± 1.4 days which was not significantly different from the survival of 11.5 ± 1.4 days we observed for unfed individuals (Two-way factorial ANOVA, $F = 0.99$, $P = 0.33$) (Table 3). We were also able to locate spiders in the thistle 14.6 ± 1.5 days and in the grass 10.7 ± 1.2 days, but this difference was not significant at the 0.05 level ($F = 3.68$, $P = 0.06$) (Table 3).

Fed individuals remained at web sites an average of 12.5 ± 1.4 days which was signif-

Table 2.—Measurements (mm) of the total body length and abdomen width of female *Argiope trifasciata* in the laboratory (mean ± standard error). Fed individuals received one cricket (150 mg) whereas unfed individuals and those that produced eggsacs received no food.

Status	n	First measurement		After 24 hours		Difference	
		Length	Width	Length	Width	Length	Width
Fed	9	14.1 ± 0.8	7.1 ± 0.5	14.5 ± 0.7	8.5 ± 0.5	+0.4 ± 0.2	+1.3 ± 0.1
Unfed	13	15.2 ± 0.5	7.8 ± 0.4	15.0 ± 0.6	7.6 ± 0.4	−0.2 ± 0.2	−0.2 ± 0.2
Produced eggsac	6	14.1 ± 0.8	7.4 ± 0.4	12.5 ± 0.4	5.8 ± 0.4	−1.6 ± 0.2	−1.5 ± 0.2

Table 3.—Results of prey manipulation experiment in which fed spiders in thistle and grass were compared to spiders left to natural prey capture. Morphological measurements (abdomen width and total length) represent the difference between the fourth day after prey supplementation began and the sixteenth day after supplementation began. Data are expressed as mean ± standard error.

	Fed	Unfed	Treatment	Vegetation	Interaction
Change in abdomen width (mm) in 12 days	($n = 10$)	($n = 10$)	$F = 3.61$ $P = 0.08$	$F = 0.24$ $P = 0.63$	$F = 1.04$ $P = 0.32$
Grass ($n = 7$)	1.50 ± 0.03	1.15 ± 0.55			
Thistle ($n = 13$)	2.18 ± 0.46	0.94 ± 0.20			
Both habitats	1.80 ± 0.30	0.98 ± 0.18			
Change in body length (mm) in 12 days	($n = 10$)	($n = 10$)	$F = 1.22$ $P = 0.28$	$F = 1.91$ $P = 0.19$	$F = 0.08$ $P = 0.78$
Grass ($n = 7$)	0.64 ± 0.73	0.10 ± 0.50			
Thistle ($n = 13$)	2.06 ± 0.54	0.83 ± 0.45			
Both habitats	1.19 ± 0.45	0.68 ± 0.38			
Total days located	($n = 26$)	($n = 30$)	$F = 0.99$ $P = 0.325$	$F = 3.68$ $P = 0.061$	$F = 1.71$ $P = 0.187$
Grass ($n = 30$)	11.0 ± 1.8	6.8 ± 1.2			
Thistle ($n = 26$)	14.3 ± 2.3	10.8 ± 2.2			
Both habitats	13.1 ± 1.8	8.6 ± 1.6			
Web relocations per spider	($n = 26$)	($n = 30$)	$F = 5.60$ $P = 0.022$	$F = 0.12$ $P = 0.750$	$F = 2.98$ $P = 0.09$
Grass ($n = 30$)	0.3 ± 0.1	0.4 ± 0.2			
Thistle ($n = 26$)	0.0 ± 0.0	0.6 ± 0.2			
Both habitats	0.2 ± 0.1	0.5 ± 0.1			

icantly longer than the unfed spiders which remained only 8.7 ± 0.2 days. This difference verifies that fed spiders had significantly fewer web relocations (Two-way factorial ANOVA, $F = 6.99$, $P = 0.011$) (Table 3). Spiders in the thistle relocated their webs with the same frequency as the spiders located in the grass ($F = 0.0001$, $P = 0.95$) (Table 3).

DISCUSSION

An increase in prey capture by adult female *Argiope trifasciata* influences the decision to relocate or continue foraging in the same web site. These data are consistent with the results of Olive's (1982) enclosure experiments in which *A. trifasciata* individuals tended to leave areas in enclosures where food was not provided and aggregate in regions where food was supplemented. The fact that we were able to quantify an increase in spider condition via morphological measurements verifies that the food we were providing was sufficient to affect the spiders and provides a close link to food as the mechanism causing the changes in behavior we observed. The fact that we could take these hunger measurements in the field without disturbing the spider is a desirable feature of this system. Since we were able to demonstrate that there was no impact of habitat or manipulation on these measures, only the supplemental prey that we provided can account for the differences we observed. Numerous studies have associated prey capture with web site tenacity (Turnbull 1964; Janetos 1982; Olive 1982; Riechert & Gillespie 1986; Gillespie 1987; Vollrath 1987; Rubenstein 1987; Bradley 1993 and references therein) but the quantification of prey capture in the past has always been prey in the web rather than some measure of actual intake by the spider as we were able to accomplish.

One possible confounding factor that might affect our morphological measurements would be the production of an eggsac which substantially reduces the spider's abdomen size and changes its appearance. However, we did not observe the same kind of emaciation after egg laying in individuals we were monitoring
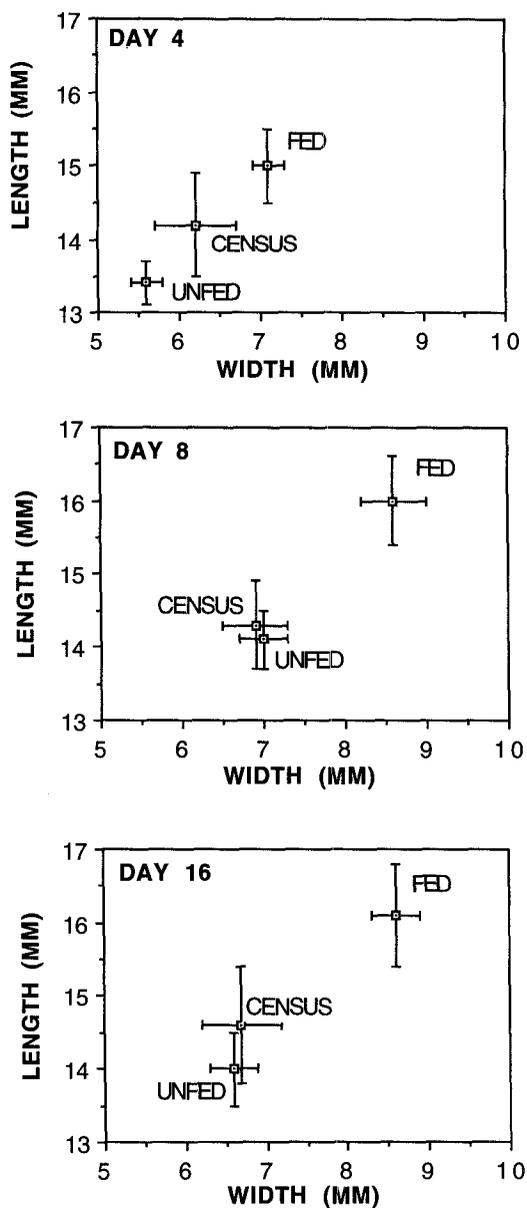
Figure 1.—Total body length and abdomen width (mean ± SE) of spiders measured 4, 8 and 16 days after prey supplementation was begun. On Day 4, abdomen width was significantly different among groups ($F = 4.43$, $P = 0.003$) whereas total body length was not ($F = 2.3$, $P > 0.05$). On Day 8, both abdomen width ($F = 3.95$, $P = 0.007$) and total body length ($F = 2.6$, $P = 0.048$) were signficantly different among the treatments. On Day 16, abdomen width was signficantly different ($F = 4.25$, $P = 0.0085$) but total body length was not ($F = 1.389$, $P > 0.05$).

in the field that we saw in laboratory spiders. Since eggsacs are deposited very late in the season and since this species produces only one clutch per year (Tolbert 1976), it is likely that the spiders were dying shortly after the production of their egg sacs in the field, perhaps due to an increase vulnerability to predation or other environmental stressors. In any case, we would predict that the spiders receiving food supplements would be most likely to produce eggs since food intake is positively correlated with egg production in many species of spiders (Wise 1993 and reference therein). Therefore, if egg sac production were confounding our results, it would have reduced the likelihood of seeing the significant differences in body size we observed between the food supplemented and unsupplemented spiders in this study.

Spiders are frequently categorized as food limited in nature because they can survive long periods of starvation (Anderson 1970, 1974), have low metabolic rates (Anderson 1970; Carrel & Heathcote 1976; Nakamura 1987), and the fact that they tend to aggregate in high prey areas (Olive 1982; Rypstra 1989). It has been suggested that the plasticity of the abdomen in spiders is an adaptation to prey shortages because it enables spiders to consume large amounts of prey when it is abundant and store it for subsequent lean periods (Wilson 1971; Anderson 1974). Since the ability of a spider's abdomen to expand with consumption should decrease as it reaches its maximum, the substantial morphological changes we observed suggested that the spiders in our population were not close to satiation. Likewise the fact that manipulating the prey they consumed altered their web site tenacity provides further evidence that food is a limiting resource for this web-building spider (Wise 1993).

Food supplementation had more consistent effects on the spider's abdomen width than on total body length (Fig. 1). The abdomen is flexible and therefore changes size with feeding, whereas the cephalothorax is fixed in size for a given instar. Of our measurements, abdomen width is a more direct measurement of the changes in condition the spider experienced since any abdominal changes reflected in total body length are damped by the cephalothorax size, which cannot change. As a result, we saw less consistent differences among

treatments over the course of the experiment in body length than in abdomen width. In retrospect, a more accurate assessment of spider condition would have been obtained if we had taken measurements of the cephalothorax alone or some other body part that we knew did not change with feeding. Then we could have scaled body condition on absolute body size as recommended by Jakob et al. (1996).

Optimality theory predicts that the amount of time an organism remains at a site should be related to some combination of prey capture at that site and their investment in that site (Pyke et al. 1977). If this is true then, in a given habitat, spiders with more energetically costly webs should have longer web residence times since it should take them longer to recoup the investment in the web itself (Janetos 1986; Riechert & Gillespie 1986). The residence times that we recorded for unsupplemented A. trifasciata were around 8.5 days which is substantially longer than the time reported (3 days) for a wide variety of other orbweaving spiders (Janetos 1982; Olive 1982; Riechert & Gillespie 1986; Smallwood 1993). Even the linyphiids with semi-permanent webs that Janetos (1982) studied had residence times around 5 days. In contrast, residence times of the linyphiid with a semi-permanent web, Neriene radiata (Walckenaer 1844), were about 10 days; a value much closer to those we observed in A. trifasciata (Martyniuk 1983). Since A. trifasciata has a large web and reuses some portion of the support infrastructure, the construction of an entirely new web in a new location may be more costly than the other orb-weavers investigated. The large body size of this spider at late instars prevents from moving by ballooning and it appears to walk awkwardly off of the web. As a result, exploring for new web sites is a risky and energetically costly endeavor for A. trifasciata.

When spiders reach high densities then interactions with one another can influence web site tenacity (Hoffmaster 1986; Rypstra 1985; Smallwood 1993). It seems unlikely that web take-overs or spider interactions on the webs were factors in this study. In experimental plots the spider density was only 0.05 individuals per m² in the thistle and 0.06 individuals per m² in the grass and the spacing was fairly uniform across the plots. The low densities in these experiments and the fact that

we never observed individuals moving more than two m in a web relocation event (McNett 1995), suggest that intraspecific interactions were not very important in our these experiments. Additionally, it may be that the low densities with which we were working and the elimination of spider-spider interactions as a disturbance, accounts for the relatively long residence times that we observed compared to other orb-weaving spiders.

The size and web relocation behavior of A. trifasciata in the grass and thistle habitats we compared were surprisingly similar. Prey capture of spiders in thistle must have been similar to that in the grass because we uncovered no morphological differences in the spiders inhabiting the two habitats (Table 2). This result is supported by our captures in insect traps which failed to reveal any differences between these two habitats in prey activity at this time in the season. Since Enders (1975, 1976) related web relocation to destruction by wind, we expected to see more relocation events by spiders living in grass since it offers a less sturdy web support than thistle. Perhaps, at least in the season of this study, wind was not sufficiently damaging to affect the spider's behavior.

Although not significant at the 0.05 level, it is tempting to speculate on the nearly significant difference in survival between animals in the thistle and those in the grass ($P = 0.06$, Table 2). Indeed, since we were monitoring such a short period in the end of the spider's life, it is surprising that there is any suggestion of a difference by habitat in the timing of their death at the onset of winter. Horton (1980) found that Argiope in North American old field habitats are subject to substantial bird predation and that the zig-zag stabilamentum offers them some protection from birds. For those of us who have monitored spiders in thistle habitats, it is not difficult to believe that the irritating leaves of this plant could provide the spiders some protection from a variety of vertebrate predators which may have contributed to the near significant difference in survival we observed.

In summary, these data demonstrate that change in prey intake is a major factor influencing web site tenacity of these large orb-weaving spiders. The difference in body condition between spiders that received supplemental prey and those that did not was the

overriding difference between the spiders studied here even though we also compared spiders in two structurally different old field habitats. The ease with which we could verify changes in body condition make detailed analysis of the impact of food intake on the ecology and behavior of *A. trifasciata* in a natural setting possible.

ACKNOWLEDGMENTS

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