DIFFERENCES FACILITATING THE COEXISTENCE OF TWO

SYMPATRIC, ORB-WEB SPIDERS, ARGIOPE AURANTIA LUCAS

AND ARGIOPE TRIFASCIATA (FORSKAL) (ARANEIDAE, ARANEAE)

by
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APPROVAL SHEET

Title of Thesis: Differences facilitating the coexistence of two
sympatric, orb-web spiders, <u>Argiope</u> <u>aurantia</u> Lucas
and <u>Argiope</u> <u>trifasciata</u> (Forskal) (Araneidae, Araneae)

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ABSTRACT

Title of Thesis: Differences facilitating the coexistence of two sympatric, orb-web spiders, <u>Argiope aurantia</u> Lucas and <u>Argiope trifasciata</u> (Forskal) (Araneidae, Araneae)

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Two closely-related, sympatric, orb-web spiders, <u>Argiope aurantia</u> and <u>Argiope trifasciata</u>, take prey which differ in size. In accordance with the often-assumed direct relationship between the size of predators and their prey, <u>A</u>. <u>aurantia</u> is larger than <u>A</u>. <u>trifasciata</u> at any single point in time, largely a result of their asynchronous reproductive cycles. The ratio of their sizes exceeds the 1.28 proposed by Hutchinson (1959) for coexistence. Vertical and horizontal differences in their use of the microhabitat also occur and may further reduce the overlap in their use of food or reduce the frequency of interspecific interactions. In this study, vertical stratification of webs occurred only late in the season, with <u>A</u>. <u>aurantia</u> higher than <u>A</u>. <u>trifasciata</u>. These results contrast with those of Enders (1974), probably due to different densities of the two species in our study areas.

Experiments show that the differences in the size of prey taken by these <u>Argiope</u> spiders were due, in part, to dissimilarities in the filtering properties of their webs and to differences in the ability of the two species to capture prey of the same relative size. However, the differences were mainly due to the spiders' rejection of a large and different portion of the available prey.

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INTRODUCTION

Closely-related, sympatric species have often been found to differ in their utilization of resources. For example, among the dissimilarities found to occur between closely related birds in the same habitat were differences in their size, food, and feeding location (Lack 1944; MacArthur 1958; Cody 1968). Anolis lizards examined by Schoener (1968, 1970) and Schoener and Gorman (1968) differed in their size, food, insolation preferences, perch height and perch diameter. Hutchinson (1959) suggested that differences in the size of closely-related, sympatric animals often resulted from asynchronous reproductive timing and led to differences in the size of the prey they used.

Partitioning of resources by web-building spiders has seldom been studied in spite of the fact that these spiders are excellent subjects for investigation of the use of food and space. This suitability is due to their abundance, the stationary nature of their webs and the way in which they feed (i.e., digestion is external to the spider's body and occurs on the web). Enders (1974), however, did examine the use of space by two congeneric, co-occurring, orb-web spiders: Argiope trifasciata (Forskal) and Argiope aurantia Lucas. He found that, when they were immature, they placed their webs at different heights (Enders 1974). In addition, he observed each species invading the webs of the other and hypothesized that web invasion was the proximal cause of their web placement pattern. Enders (1974) also analyzed information in the literature on sympatric European araneid spiders and concluded that they coexist by differences in their breeding cycles, size and the size of their prey. A. aurantia and A. trifasciata differ in

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their breeding cycles; however, he believed that they were taking similar prey and therefore were able to coexist because of vertical stratification.

Although these Argiope species are reported to be subject to predation (Comstock 1940; Enders 1974) and the effects of weather (Levi 1968), I found both species to be abundant in an old-field habitat. Consequently, I was able to test the hypotheses that (1) A. aurantia and A. trifasciata use different-sized prey, and that (2) the two species of spider differ in size. Verification of these hypotheses would suggest that food partitioning is an important mechanism for their coexistence and would substantiate the assumption, which is often made, that a direct relationship exists between the size of predators and the size of their prey.

Schoener (1970, 1974) noted that closely-related, co-occuring species may differ in more than one niche dimension. His studies of Anolis lizards indicated that differences in feeding structures, horizontal and vertical division of space, and different climatic preferences may all operate at the same time (Schoener 1970). In order to determine if differences between A. aurantia and A. trifasciata were also multidimensional, I investigated the possible existence of web stratification and food partitioning by taxa in the Argiope populations inhabiting my study area.

Wilson (1975) has questioned whether size differences of predators provide a sufficient means of niche separation. According to his argument, prey too large for small predators would be available to the larger, whereas the reverse would not be true. This could bestow a competitive advantage upon the larger animal. On the other hand,

optimal feeding theory provides an explanation for why a larger predator should take fewer small prey than a smaller predator (Emlen 1966, 1973; MacArthur and Pianka 1966; Schoener 1971). If this theory applies to the _Argiope_ species, their foraging methods lead one to question how the prey-size composition of their diet is determined. Therefore, I designed experiments to investigate how the spider and the web influence what sizes of prey are captured by _A_. _aurantia_ and _A_. _trifasciata_.

NATURAL HISTORY OF THE TWO ARGIOPE SPIDERS

A. aurantia and A. trifasciata, known respectively as the black
and yellow garden spider and the banded garden spider, are found
throughout North America (Levi 1968; Kaston 1972), usually in the same
old-field habitat (Bilsing 1920; Levi 1968; Enders 1973). Their
general morphology and feeding structures are similar (Levi 1968).
The body length of mature females of both species is approximately
25 mm, and that of mature males is approximately 5-6 mm.

Mating occurs in late summer, and the males die soon after.
Females of both species lay eggs in late summer or early fall and
encase them in a cocoon (approximately 1000 eggs / cocoon), which is
suspended from vegetation. A. aurantia hatch from eggs several weeks
after they are laid and overwinter within the cocoon as spiderlings
(Levi 1968; Enders 1974), whereas A. trifasciata are reported to over-
winter as eggs and hatch several weeks before emergence from the
cocoon (Tolbert pers. comm.). Both species emerge as second instar
spiderlings in the spring, with A. aurantia preceding A. trifasciata
by several weeks (Enders 1974; Tolbert pers. comm.).

Their similar orb-webs are built almost vertically, contain a
viscid spiral thread, and usually have zig-zag stabilimenta across the
hub. Barrier webs, constructed parallel to one or both of the flat
surfaces of the web, may also be associated with the orb web. No
retreat is built, and the Argiope inhabiting the web is usually
located head-down at the hub.

The impact of an insect in the web usually elicits predatory
behavior (Harwood 1974; per. observ.). These spiders typically
capture prey by wrapping it in silk and then administering a series of

bites in which venom is injected (Harwood 1974). The sequence is reversed for lepidopteran prey and is further modified for small prey which are first given a crushing bite and then carried to the hub where a minimum of silk is used to allow attachment to the web (Harwood 1974).

METHODS

Field Study

In a community containing populations of both Argiope species, I
periodically measured the size of the spiders, the size of their prey
and the height of their webs in order to test the hypotheses that these
sympatric populations of Argiope spiders differed significantly with
regard to these parameters. In order to determine if prey size was
more closely correlated with the spider's size than with other
variables, I measured additional parameters. These parameters were:
height of web, height of vegetation to which web was attached, maximum
height of vegetation within one meter of web, height of vegetation
beneath web, and time.

I conducted the study in three adjacent fields located at the
Smithsonian Institution's Chesapeake Bay Center for Environmental
Studies at Edgewater, Anne Arundel County, Maryland. The fields are
bordered by dirt roads and contain a variety of herbaceous plants
including goldenrod (Solidago spp.), tickseed-sunflowers (Bidens spp.),
black-eyed susan (Rudbeckia hirta), partridge-pea (Cassia fasciculata),
bush-clover (Lespedeza spp.), tick trefoil (Desmodium spp.), honey-
suckle vines (Lonicera sp.), various grasses, and blackberries (Rubus
alleghensis). The fields also contain young sweet-gum (Liquidambar
styraciflua), pine (Pinus virginiana), and cherry (Prunus sp.) trees,
none taller than 3-4 meters in height.

I collected data from August 28 to October 14, 1975, and from July
14 to September 24, 1976. In 1975, I traversed alternate rows of marked
10-meter square quadrants within an 80 by 60 meter area in one of the
fields. I entered the study area in a different direction and at a

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different, randomly-chosen place at the start of each complete survey. In 1976, I sampled an area approximately 750 meters long and 10 meters wide, which was located along the dirt roads. At the beginning of the survey period, I determined that the Argiope aurantia population was smaller than the A. trifasciata population. I marked the A. aurantia webs that could be found within the study area at this time by tying colored yarn to the vegetation to which the webs were attached. I also marked an equal number of A. trifasciata web sites. In order to facilitate locating webs, I used a compressed air sprayer to spray a fine mist of water on areas being searched. Marked webs were checked weekly between 1000 and 1900 hours. At each sampling I began at a different, randomly chosen point along the roads, changing direction and the side of the road at each start. If I observed a prey item on a web, I ordinarily collected it, measured and recorded the following parameters: body length of spider (not including appendages), height of vegetation below web, distance from center of hub to the ground, height of vegetation to which web was attached, and height of tallest vegetation within one meter of web. I recorded the order to which the prey belonged and the length and width of its body. However, when the order to which the prey belonged could be determined without removing it from the web, I measured it while on the web to minimize possible effects of reducing the food supply of the spiders. If fewer than 15 individual prey items were recorded in one day for either species of spider, I returned the next day, when possible, to continue the sampling. In the interest of clarity, when two days were used for a sample, I will refer only to the first day; if they were not consecutive days, I will refer to the day nearest their midpoint. Additional

webs were marked each week to replace those marked webs that had disappeared or which no longer contained a resident Argiope.

I computed means and standard deviations for all parameters measured, and the parameters were tested for significant differences between the species using analysis of variance. Correlations and partial correlations were determined between prey size and the other variables listed above.

Length is the most common measurement used in comparing the size of arthropods. However, variations in the ratio of length to width among prey items indicated that length alone is a poor measure of the relationship between the size of a spider and the size of its prey. Consequently, I used $\sqrt{\text{body length X width}}$, which provides a standardized, linear measure that takes both length and width into consideration.

I used a contingency table and G-test (Sokol and Rohlf 1973) to analyze the frequency with which each prey order occurred in the sample to determine if there was a significant difference in the orders taken by the two Argiope species.

On July 17-18, 1976 and again on August 19, 1976, I counted, weighed and measured all the A. aurantia and A. trifasciata within a 100 square meter area in order to compare simultaneous changes in population density and individual growth.

The essentially rectangular spaces which occur between the strands of a web are referred to as the mesh of the web. On July 24, 1976, I measured the shorter dimension (width) of the mesh at a position approximately half way between the center and upper edge of the webs.

Experiments

I designed experiments to investigate how the <u>Argiope</u> spiders and their webs influence what size of prey is captured. Since less than one prey item per hour contacted a web in natural populations (personal observation), it was impractical to make direct observations on these variables. I ran experiments between July 28 and October 9, 1976. Six female <u>A</u>. <u>aurantia</u> and six female <u>A</u>. <u>trifasciata</u> spiders were placed, one spider per cage, in outdoor wood and fiberglass-screen cages measuring 44 cm X 44 cm X 22 cm. When spiders died, I replaced them. Branches placed in the cages facilitated web building by smaller spiders. When the spider was large enough for its web to span the cage, I removed the branches.

After offering a prey item to a spider, I observed the results to determine if the web held the prey long enough for the spider to respond to the prey, if the spider made an attempt to capture the prey item, and if the spider succeeded or failed in the attempt. The length and width of the prey item, the order to which the prey belonged and the events which led to capture or escape of the prey were recorded. Since measuring spiders before an experiment might unduly disturb them, I measured the spiders after the first experiment of the day. At this time, captured prey were not yet ingested; consequently, the size of the spider's abdomen was not affected by recent food intake. I offered no prey item to a spider which had prey on her web or to which prey had been offered within the previous two hours.

Comparisons were made on the basis of a relative-size ratio, computed as $\sqrt{\text{prey's body length X width}} / \sqrt{\text{spider's body length X width}}$. The generation of samples within ten relative-size categories (from

$<$.25 to 2.50 X the size of the spider) required prey whose size range ran from approximately 3 mm X 1 mm to 30 mm X 7 mm. The prey taxa used to cover this range belonged to the following orders: Diptera (<u>Drosophilia</u> <u>melanogaster</u>), Orthoptera (crickets and grasshoppers), Homoptera (<u>Graphocephala</u> spp.) and Coleoptera (<u>Tenebrio</u> sp.). These prey were from taxa which were known, either from preliminary experiments or from field observation, to be acceptable to both species. The Diptera were laboratory raised as were the Coleoptera, and the balance of prey offered were captured in the field by sweep netting.

Because the spiders were not of uniform size and were growing during the testing period, all orders of prey could be used to represent most of the relative-size classes in experiments involving both <u>Argiope</u> species. Although the data were analyzed on the basis of relative size-class increments of .50, care was taken to have adequate samples within .25 increments in order to insure that all portions of the .50-increment size classes were represented in the results.

One would expect factors other than the size of prey to influence the spider's ability to capture prey. For example, characteristics of particular prey taxa could very well prove advantageous or disadvantageous to either of the spider species. Intraspecific differences in prey-capturing ability may also occur. For example, some orb-weaving spiders grow in an allometric fashion (Witt and Baum 1960; Reed, Witt, Scarboro 1969). The possible variation in the ratio of one body part to another during a spider's life may result in differences in their ability to capture prey. Experience may also differentially affect the spider's success. Consequently, data were also analyzed on the basis of success with different taxa and success of small ($\sqrt{\text{length X}}$

$\overline{\text{width}}$ = 2-8 mm) versus large ($\sqrt{\text{length X width}}$ = 8-15 mm) spiders.

Statistical Tests

Transformations were performed or non-parametric tests were employed where assumptions of parametric tests were not met. Tests are two-tailed unless otherwise noted, since there was no a priori reason to exclude one direction in results. I used contingency tables and G-test (likelihood ratio test)(Sokol and Rohlf 1973) where the test is not designated in results.

Spiders and Prey; Size and Taxa

A. aurantia was larger than A. trifasciata in each of the weeks sampled (Fig. 1, Appendix 1). This difference was significant for each week sampled in 1976 and for four of the six weeks sampled in 1975. Since only one A. aurantia was sampled during the first sampling week in 1975, that week could not be analyzed. When I combined the 1975 data because of small sample sizes of A. aurantia, the difference was also significant (p<.001 in F test for ANOVA). When cephalothorax measurements were taken in mid-July, the ratio of mean cephalothorax length of A. aurantia to A. trifasciata equalled 1.35.

A comparison of 1975 and 1976 data, where sample sizes permit, indicates that A. trifasciata were larger on August 28 and September 10, 1975, than on those dates in 1976 (p < .001 in two-tailed Mann-Whitney U test)(Sokol and Rohlf 1973), but that they were not significantly different on September 24. A. aurantia, on the other hand, did not differ significantly at any of these times (Fig. 1).

Differences in size ($\sqrt{\text{length X width}}$) of prey followed the same pattern in 1975 and 1976, with A. aurantia taking larger prey than A. trifasciata. Differences were significant for one week during 1975 and for all but one week of 1976 (Fig. 2, Appendix 1).

According to May and MacArthur (1972), in order for species adjacent on a food-size resource continuum to coexist, the average size of food which each takes must differ by an amount roughly equal to the standard deviation in the size of food taken by either species (difference/SD ~1). When computed for the two Argiope species, this

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Figure 1. Lengths of spiders, A. aurantia and A. trifasciata, as
weekly means. The bars equal one SD on either side of the
mean. Numbers are sample sizes.

Figure showing length of spider (mm) over time for A. aurantia (dashed line) and A. trifasciata (solid line), plotted for 1975 (top) and 1976 (bottom).
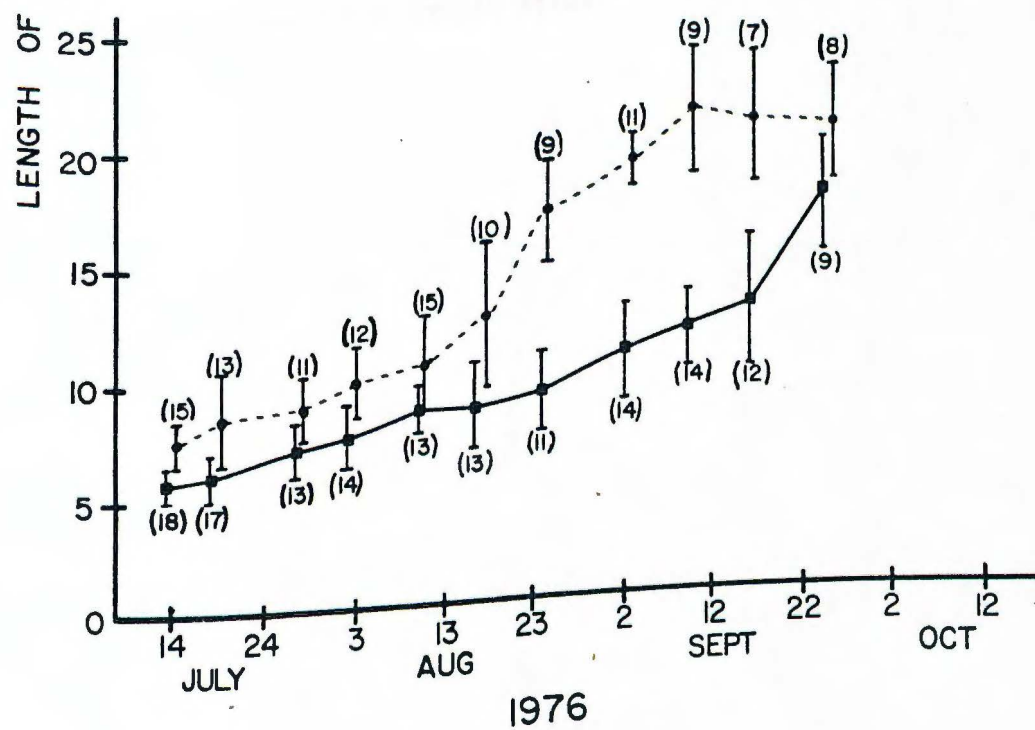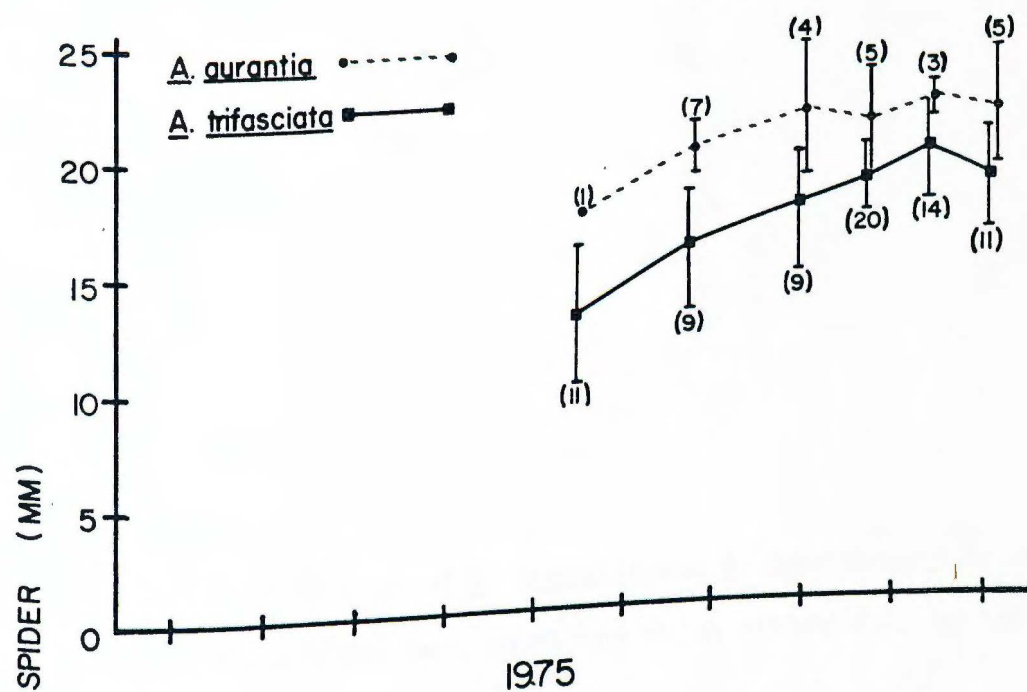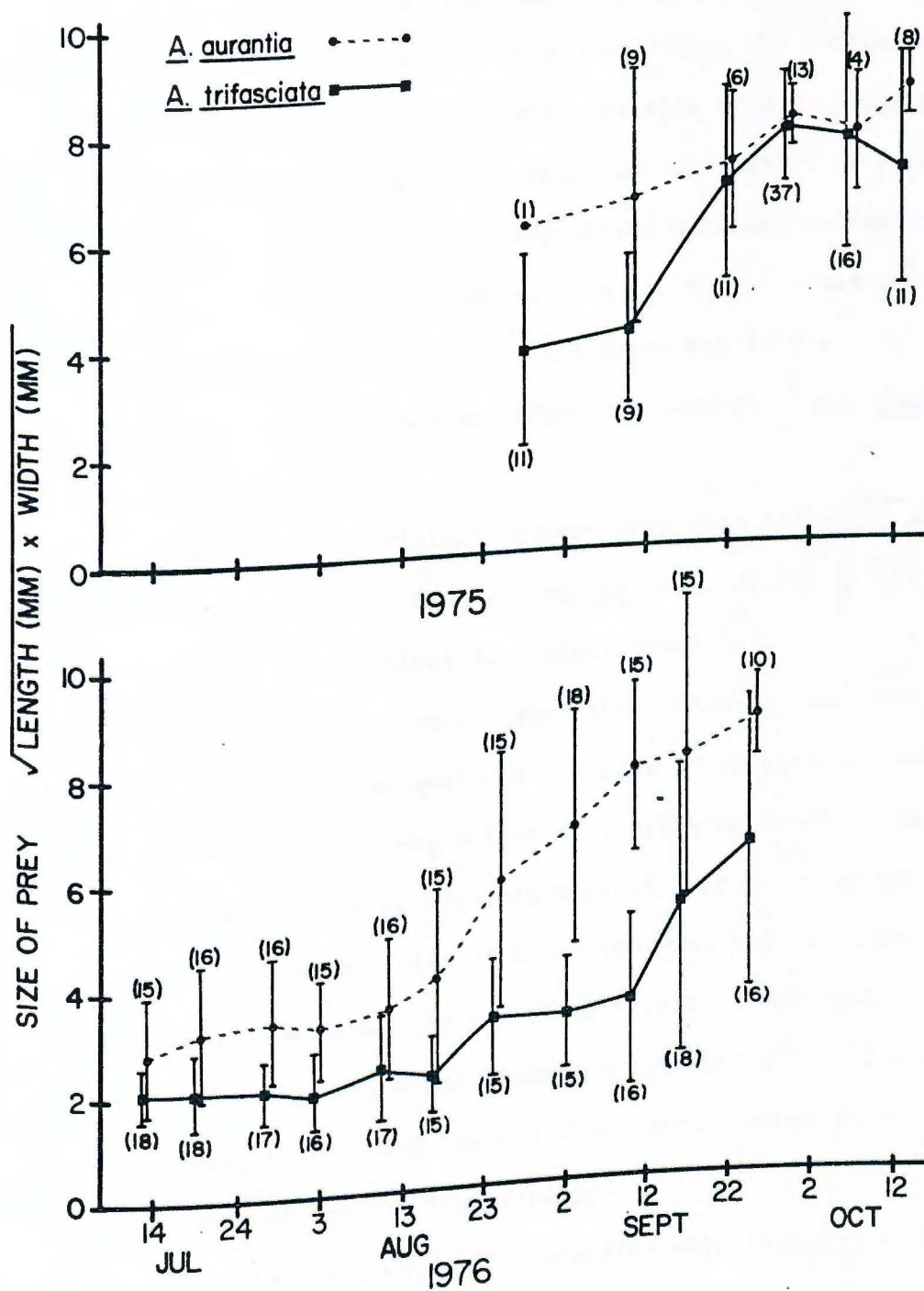
Figure 2. Size of prey of A. aurantia and A. trifasciata as weekly

means. The bars equal one SD on either side of the mean.

Numbers are sample sizes.

ratio was .93 and .94.

Figure 3 shows that, from July 14 to September 24, 1976, each size of prey up to and including 3 mm comprised an equal or greater portion of A. trifasciata's diet than of A. aurantia's, whereas the reverse was true for prey larger than 3 mm. When the months were analyzed separately, this relationship was also true for July and August, but during September, the change in utilization of prey occured at 5 mm (Fig. 4). Each month showed a larger difference between the means of the two species than did the previous month. In the graphs that are bimodal (Fig. 3 and September in Fig. 4), the right-hand mode resulted from an influx of honeybees (Apis mellifera) into the study area.

The correlation coefficient between prey size ($\sqrt{\text{length X width}}$) and spider length was .746 for A. aurantia and .594 for A. trifasciata (Table 1). These correlations were significant (p < .01 in t-test) (Sokol and Rohlf 1973) and were higher than those between prey size and any other of the variables measured: height of vegetation beneath the web, height of center of web, height of vegetation to which web was attached, maximum height of vegetation within one meter of web, and time (Table 1). When the size of the spider was kept constant, partial correlations between prey size and other variables were all non-significant (Table 1). The very small insects which the spiders ingest along with their webs, before they rebuild them, were ignored in my analysis since there were so few ($\ll$ 1/spider/day).

The two spiders did not differ significantly (p > .05) in the proportion of prey captured from different taxonomic orders (Table 2).

Figure 3.   Sizes of prey as percent of total collected from webs of
natural populations of A. aurantia and A. trifasciata
over the period July 14, 1976, to September 24, 1976.
Dashed lines equal means.   Interspecific differences in
each size class, except the 4-5 mm size class, were sig-
nificant ($p < .05$) for sizes in the range 1 mm to 9 mm.

PREY SIZE (MM) $\sqrt{\text{LENGTH} \times \text{WIDTH}}$
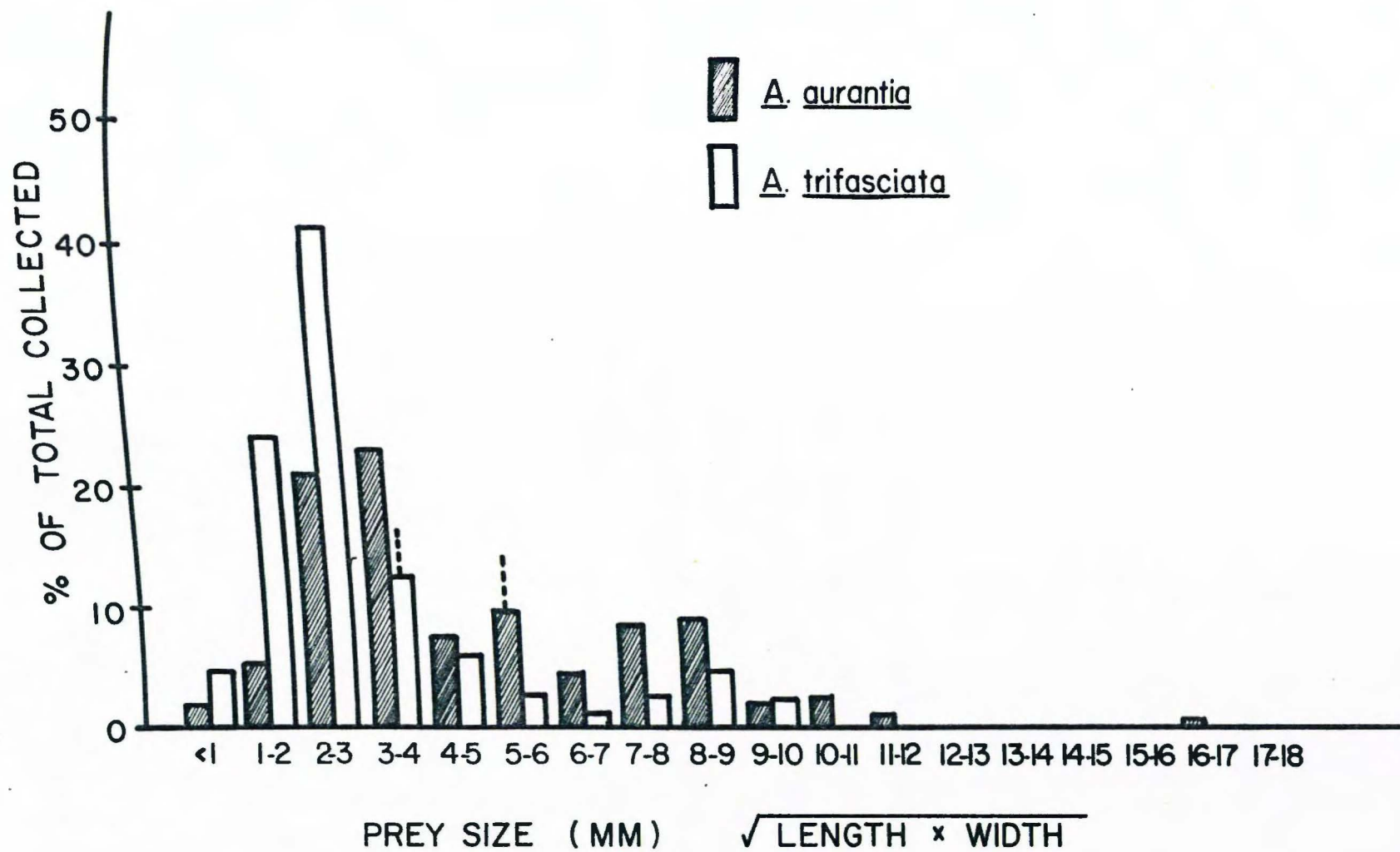
A. *aurantia*

A. *trifasciata*

Figure 4.   Sizes of prey as percent of number collected from webs

of natural populations during July, August and September

1976.   Sample sizes for A. aurantia for July, August and

September were 47, 61 and 58, respectively, and for

A. trifasciata were 53, 63 and 65.   Dashed lines show

locations of the means.

A. aurantia
A. trifasciata

JULY

AUGUST

SEPTEMBER

% OF PREY COLLECTED DURING MONTH

PREY SIZE (MM)   √LENGTH × WIDTH

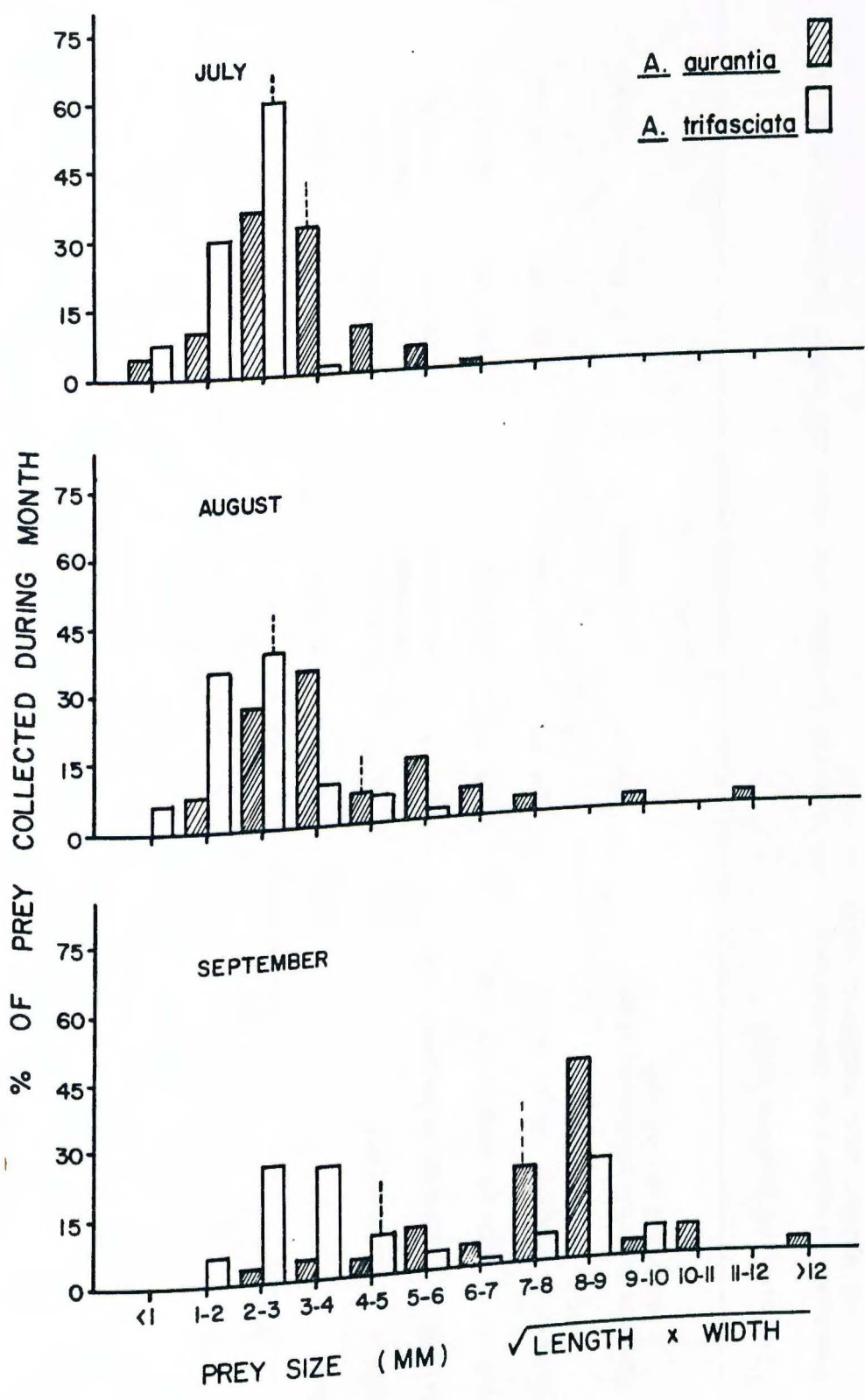<1 1-2 2-3 3-4 4-5 5-6 6-7 7-8 8-9 9-10 10-11 11-12 >12

Table 1. Correlations and partial correlations between size of prey and other variables for A. Aurantia and A. trifasciata.

Variable	A. aurantia		A. trifasciata	
	r^1	Partial[2] r	r	Partial r
Time	.673 **[3]	0.09387	.492 **	0.03394
Spider size (length)	.756 **	held constant	.594 **	held constant
Height of vegetation beneath web	.421 **	−0.04350	.301 **	0.05967
Height of web at center of hub	.504 **	−0.4564	.349 **	0.08187
Height of vegetation to which web is attached	.394 **	−0.12414	.373 **	0.08125
Maximum height of vegetation within 1 m. of web	.268 **	−0.11022	.248 **	0.05306

[1]Correlation coefficient

[2]partial correlation coefficient = correlation between prey size and other variables with size of spider kept mathematically constant

[3]correlation is statistically significant (p < .01 in t test)

Table 2. Utilization of taxa of prey by percent of total captured by A. aurantia and A. trifasciata under natural conditions.

| Taxa | A. aurantia | | A. trifasciata | |
	Sample size	Percent of total captured	Sample size	Percent of total captured
Homoptera	56	34	79	44
Hymenoptera	56	34	64	35
Coleoptera	22	13	16	9
Orthoptera	13	8	5	3
Diptera	3	2	4	2
Arachnida	4	2	4	2
Hemimptera	7	4	4	2
Lepidoptera	3	2	3	2
Neuroptera	2	1	2	1

Webs: Location and Characteristics

The height of the web refers to the distance from the center of the hub to the ground. On a weekly basis, the mean height of the webs of the two Argiope spiders differed significantly for the weeks of August 3, September 3 and 10, 1976, and September 23, 1975 ($p < .01$ in F test for ANOVA)(Fig. 5, Appendix 1). A. aurantia's webs were higher than A. trifasciata's during these weeks (Fig. 5, Appendix 1).

When compared on a monthly basis (Appendix 1), as were Enders' (1974) data, heights of A. aurantia webs were significantly greater than A. trifasciata's for August ($p < .05$) and September ($p < .01$ in F test for ANOVA) 1976 (Appendix 1).

When measured on September 15, 1976, the mean width of the mesh of 14 A. trifasciata webs was 1.85 mm (± 0.16 S.E. N=14), whereas for five A. aurantia webs it was 4.2 mm (± 0.09 S.E. N=5). The difference was significant ($p < .002$ in two-tailed Mann-Whitney U test). The mean ratios of mesh width to spider length for A. aurantia and A. trifasciata, 0.21 and 0.13, respectively, were also significantly ($p < .002$ in Mann-Whitney U test) different.

The height of the vegetation to which each web was attached was measured, as was the maximum height of vegetation within one meter of the web. On the basis of both sets of measurements, A. aurantia constructed their webs in taller vegetation than did A. trifasciata (Figs. 6, 7). These differences were significant ($p < .001$ in F test for ANOVA) for August and September 1976 and also for height of vegetation within one meter of the webs for July 1976. Differences were not significant during 1975.

Figure 5. Height above ground at which webs of A. aurantia and

A. trifasciata were located, given as weekly means. The

bars are one SD on either side of the mean. Numbers are
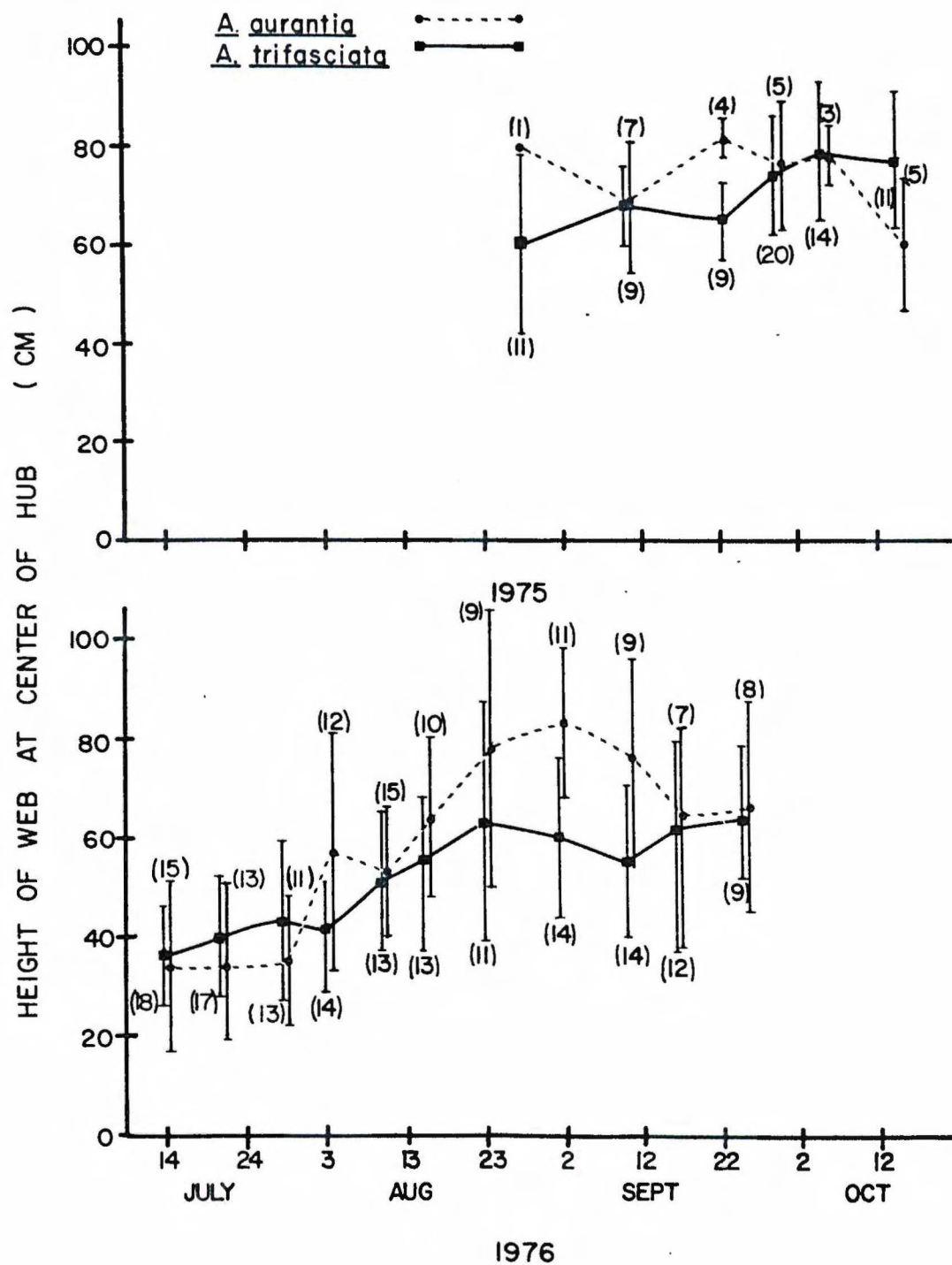
sample sizes.

A. aurantia
A. trifasciata

Figure 6. Height of vegetation to which webs were attached. Bars

are one SD on either side of the mean. Numbers in
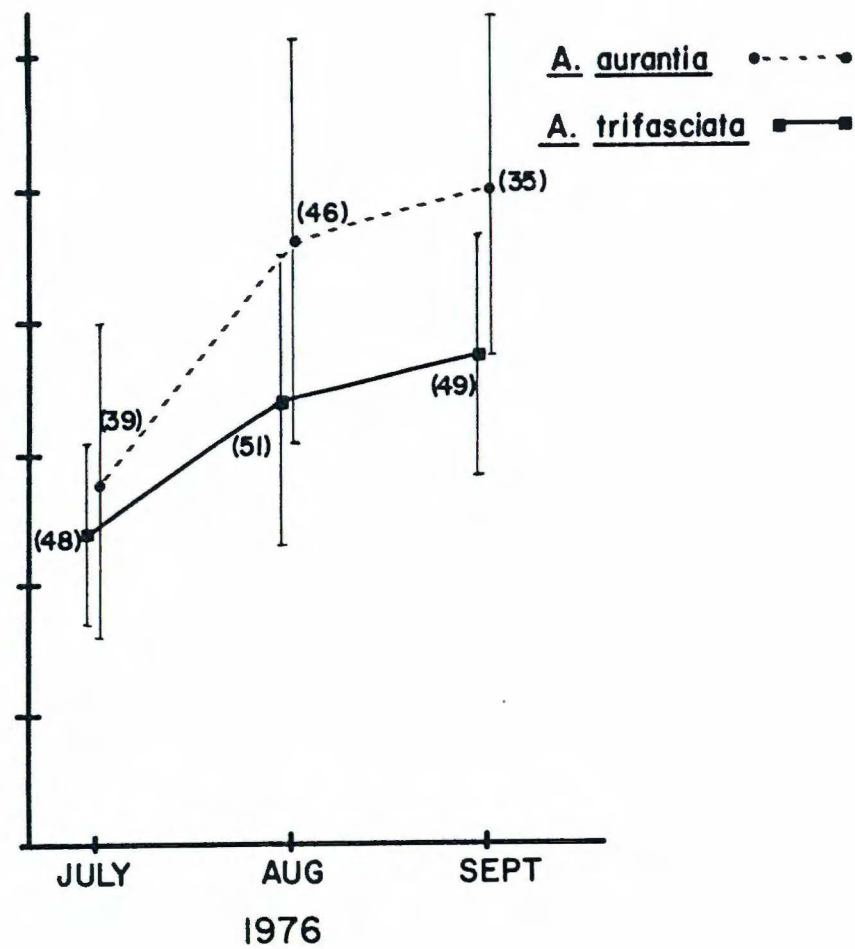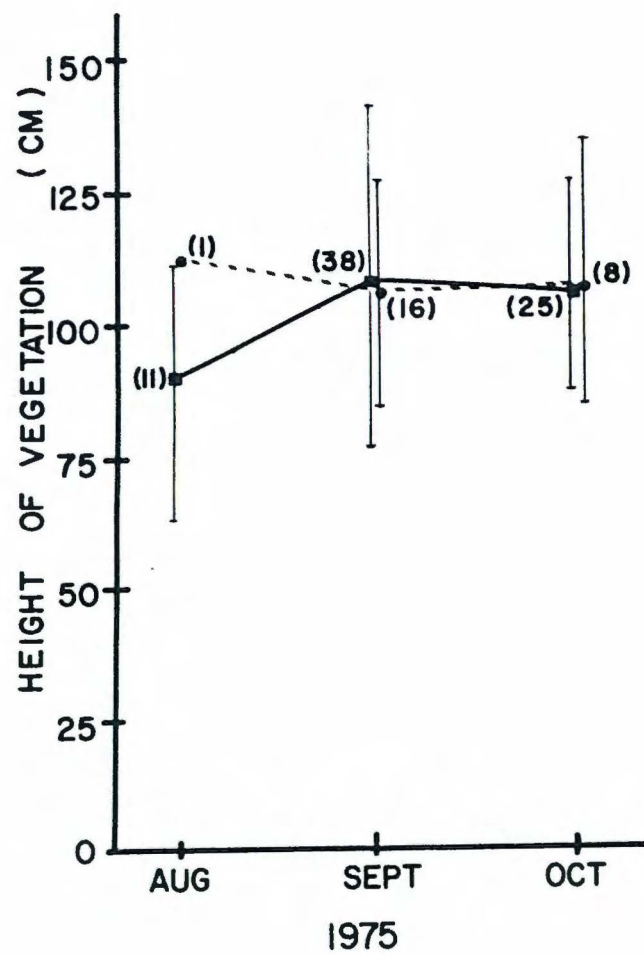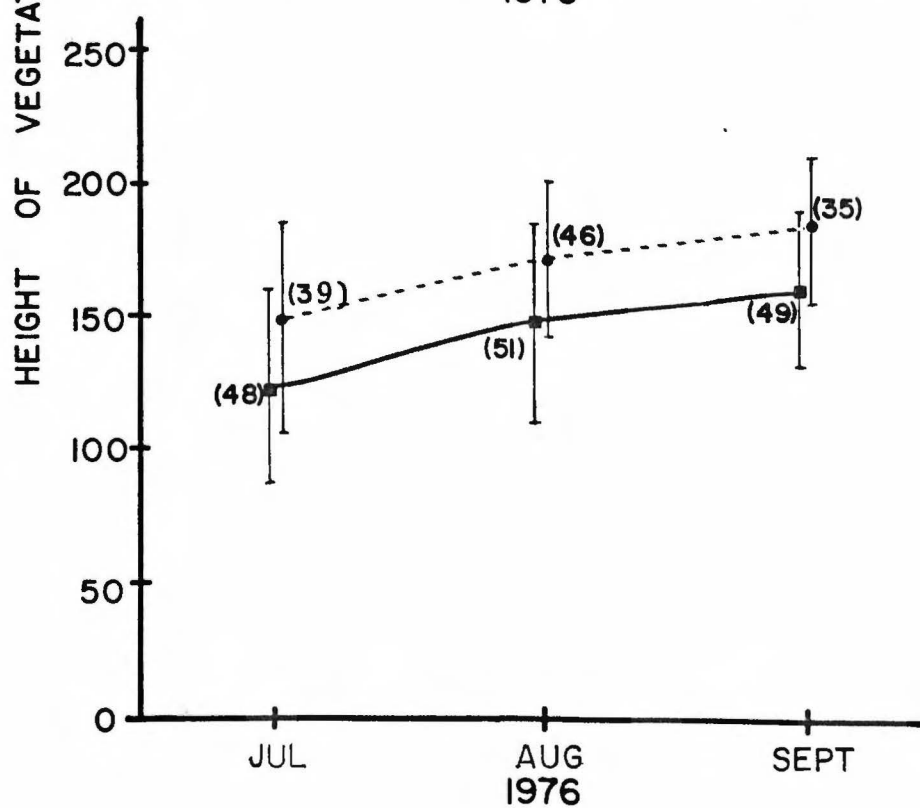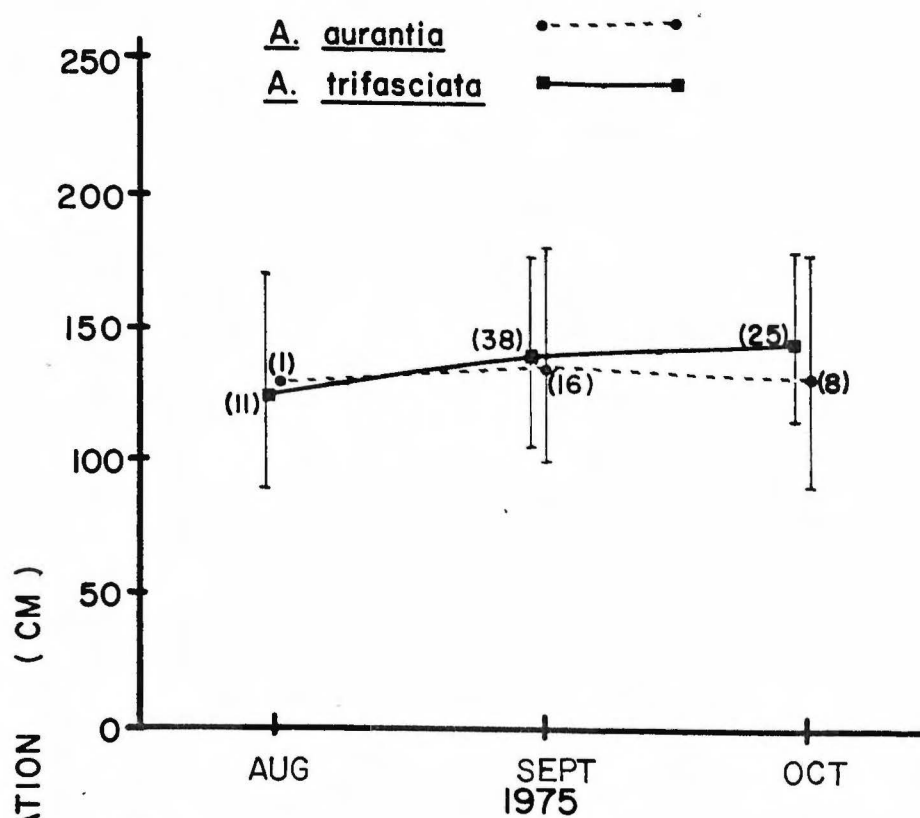
parentheses are size of samples.

Figure 7. Heights of tallest vegetation within one meter of web.

The bars equal one SD on either side of the mean. Numbers

in parentheses are size of samples.

Changes in Spider Biomass

During the period in which the spiders were studied, it became obvious that their populations were declining in the study area. Censuses taken on July 17-18, 1976, and on August 19, 1976, indicated that the A. trifasciata populations had declined from 161 spiders to 95 spiders within a 100 sq. m. area and that the A. aurantia population had declined from 9 spiders to one spider in the same area (Table 3). However, during this period, the mean weight of A. trifasciata increased more than 5 times and that of A. aurantia increased approximately 7.5 times (Table 3). Thus, within this area, there was an approximately 2.5 fold increase in Argiope biomass over a one-month period.

Experimental Results

Success Rates

I designed experiments to provide information on how the spider and the web influence which size of prey is captured. In experimental results, size refers to $\sqrt{\text{body length X width}}$. Relative size of prey is the ratio of its size to the size of the spider to which it was offered (i.e., prey/spider size ratio).

The prey offered to the spiders during the experiments were categorized as falling into relative-size classes ranging from <0.50 to 2.00-2.50 X the size of the spider. I compared the rates of success of the two Argiope species in capturing prey offered to them from each relative-size class (Fig. 8A). No significant difference occurred between the two spiders except for prey in the 1.00-1.50 range $(p< .01)$. In this class, A. aurantia captured a greater proportion of prey offered

Table 3. Change in biomass of <u>A</u>. <u>aurantia</u> and <u>A</u>. <u>trifasciata</u> within a 100 square meter area during the period July 17, 1976, to August 19, 1976.

| Date	Numbers of spiders		Mean weight/spider (grams)		Biomass per species		Total biomass
	A[1]	T[2]	A	T	A	T	
July 17, 1976	9	161	.0106 g	.0028 g	.0954 g	.4508 g	.5462 g
August 19, 1976	1	95	.0801 g	.0149 g	.0801 g	1.4155 g	1.4956 g

[1]<u>A</u>. <u>aurantia</u>

[2]<u>A</u>. <u>trifasciata</u>

Figure 8. Success rates for capture of prey of various relative

sizes by A. aurantia and A. trifasciata during experiments.

A. Success given as percent captured of number offered.

B. Success given as percent captured of number attacked.
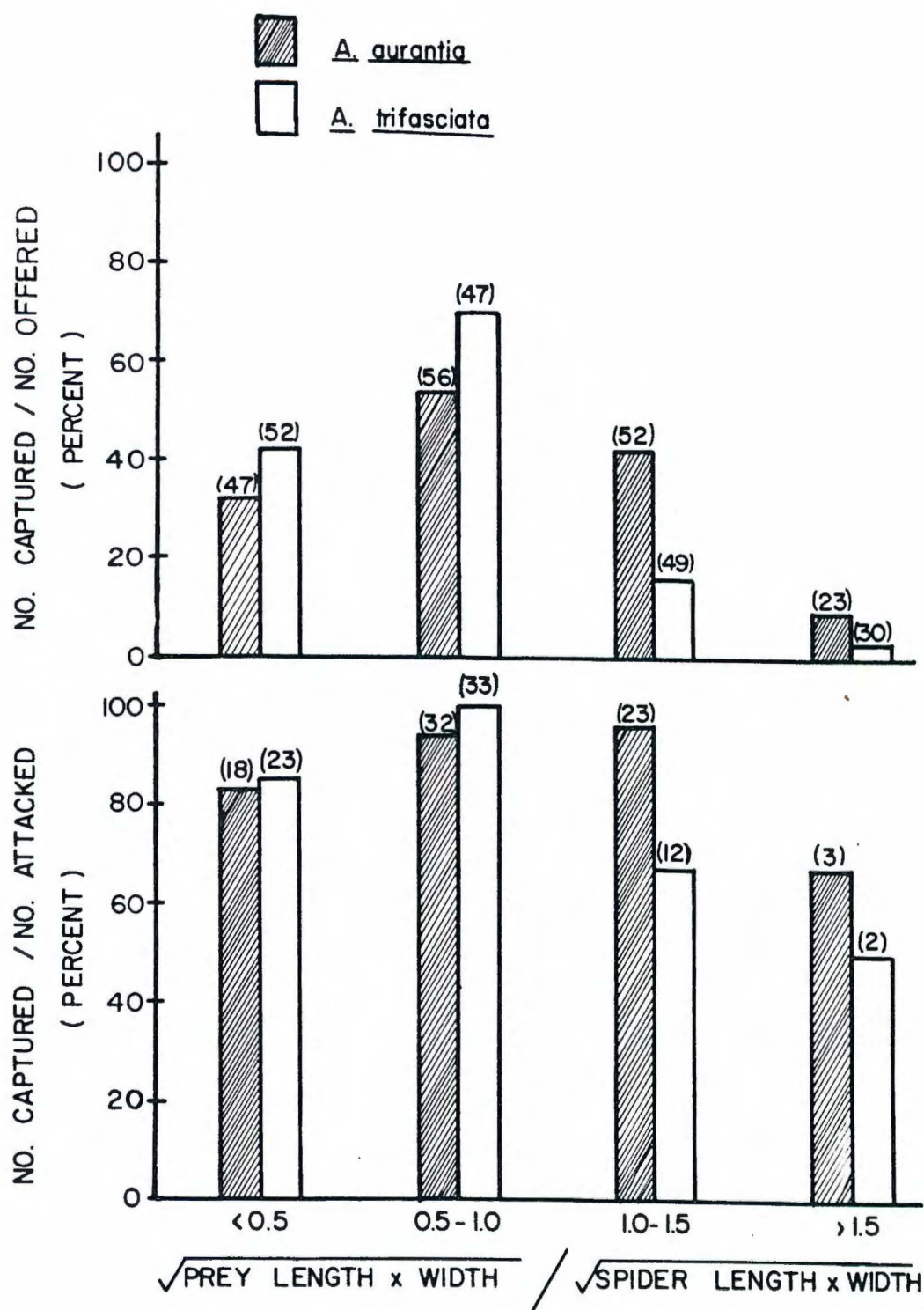
than did A. trifasciata (Fig. 8A). When all size categories were combined, the percentage of prey captured by A. aurantia and A. trifasciata, 38.8% and 35.4%, respectively, did not differ significantly. Both Argiope species captured prey whose prey/spider size ratio was in the range 0.50-1.00 with greater frequency than they captured larger and smaller prey. The lowest rate of capture occurred with prey whose prey/spider size ratio was greater than 1.50 (Fig. 8A). The mean relative sizes of prey captured by A. aurantia and A. trifasciata were 0.82 and 0.69, respectively, and were significantly different (p .01 in Mann-Whitney U test).

A more specific measure of the success rate of the spider itself is the ratio: number of prey captured/number of prey attacked (Fig. 8B). This ratio eliminates prey that were ignored, rejected, or did not adhere to the web. Using this criterion, both Argiope species were quite successful, for they both captured approximately 90% of the prey they attacked (Fig. 8B). Only one significant difference emerged: A. trifasciata captured prey whose prey/spider size ratio was 0.50-1.00 with greater success than it captured those whose ratio was 1.00-1.50 (Fig. 8B).

When, on occasion, I offered prey to spiders for the second time (no less than two hours later) on a particular day, they exhibited no greater rate of rejection than did spiders offered prey for the first time on a given day.
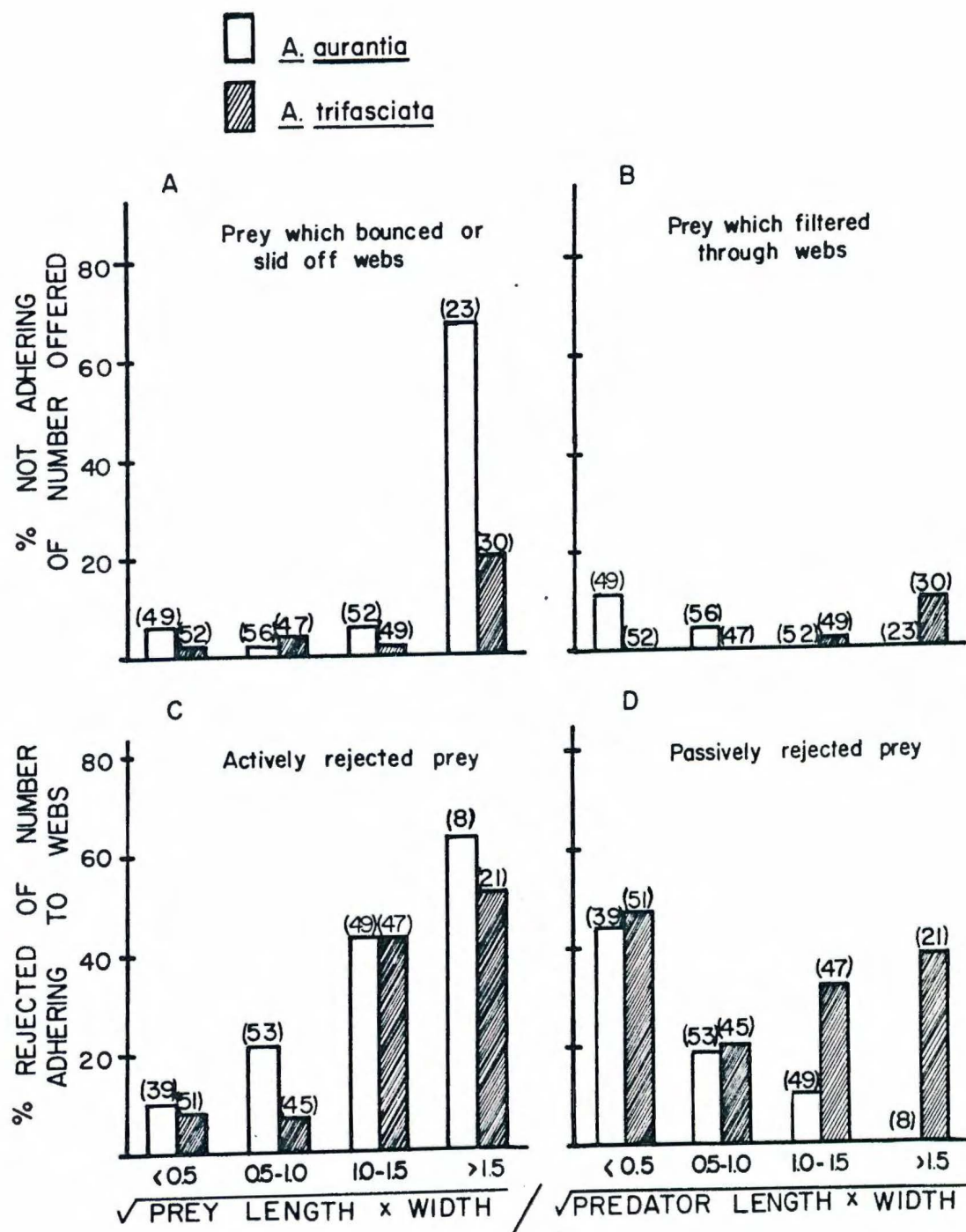
Prey Which Was Offered But Not Captured

I categorized prey which was offered but not captured in two ways. The first category included prey which slid or bounced off the web and

prey which passed through the web. The second category was comprised
of prey which adhered to the web but which: (a) were attacked but
escaped, (b) were rejected, or (c) appeared to elicit no response on
the part of the spider. The sense organs which allow spiders to
detect web vibrations are so sensitive (Bristowe 1941; Witt, Reed &
Peakall 1968; Turnbull 1973; Riechert 1976) that spiders are very
probably aware of all prey adhering to their webs. Therefore, for the
purposes of this paper, I categorized prey which appeared to elicit no
response as passively rejected or ignored, and prey which elicited a
reaction, other than an attack, as actively rejected.

Of the 178 prey items offered to $\underline{A}$. aurantia and $\underline{A}$. trifasciata,
22 and 10, respectively, slid or bounced off webs (Fig. 9A). The
difference is significant (p < .05), and reflects a highly significant
(p < .01) difference within the > 1.5 relative size class. As the size
of the prey increased, a greater percentage slid or bounced off webs
of both spider species (Fig. 9A). The number of prey which passed
through webs, 7 and 4, of the 178 offered to $\underline{A}$. aurantia and to $\underline{A}$.
trifasciata, respectively, did not differ significantly (Fig. 9B).
However, the proportion (7/103) of prey smaller than the spider which
passed through $\underline{A}$. aurantia's webs was significantly greater (p = 0.042
in two-tailed Fisher Exact Probability test) than the proportion (0/99)
which passed through $\underline{A}$. trifasciata's webs (Fig. 9B).

Approximately 49% (73/149) of the prey which adhered to webs of
$\underline{A}$. aurantia and 57% (94/164) of the prey which adhered to webs of $\underline{A}$.
trifasciata were rejected (Fig. 9C, D). The difference is not signifi-
cant. The percentages actively rejected, 28% (41/149) and 23% (38/164),
by $\underline{A}$. aurantia and $\underline{A}$. trifasciata, respectively, were not significantly

Figure 9. Variables which influence rates of success of A. aurantia

and A. trifasciata in capturing prey during experiments.

□ A. aurantia

▨ A. trifasciata

A — Prey which bounced or slid off webs

B — Prey which filtered through webs

C — Actively rejected prey

D — Passively rejected prey

% NOT ADHERING OF NUMBER OFFERED

% REJECTED OF NUMBER ADHERING TO WEBS

√ PREY LENGTH x WIDTH / √ PREDATOR LENGTH x WIDTH

< 0.5   0.5-1.0   1.0-1.5   >1.5

different (Fig. 9C). As the relative size of the prey increased, so did the rate at which they were actively rejected by both spiders (Fig. 9C).

The two Argiope species did differ significantly ($p < .05$) in their passive rejection of prey (Fig. 9D). A. trifasciata ignored prey larger than themselves with significantly ($p < .05$) greater frequency than did A. aurantia. A. aurantia ignored an increasing percentage of prey as the size of the prey decreased (Fig. 9D). However, the behavior of the spiders was similar toward prey at both extremes in relative size. A. aurantia and A. trifasciata ignored 69% (9/13) and 55% (6/11), respectively, of those prey whose prey/spider size ratio was less than 0.25, and neither spider ignored any prey whose prey/spider size ratio was greater than 1.62 (sample sizes were 15 and 14, respectively).

Success in Capturing Different Prey Taxa

Only one significant difference emerged in the success of the two Argiope species in capturing prey of various relative size classes within the different taxa of prey used (Fig. 10): A. aurantia captured a larger percentage ($p < .01$) of orthopteran prey which were 1.0-1.5 X the size of the spider than did A. trifasciata (Fig. 10).

Success Rate for Large vs. Small Spiders of Both Species

Success rates for spiders of the same size but of different species were more alike than were those for different sized spiders of the same species. Large A. aurantia were significantly ($p < .05$) more successful than large A. trifasciata in capturing prey whose prey/spider size ratio was 1.0-1.5 (Fig. 11). However, small and large A. trifasciata differed significantly in their success in capturing prey

in two relative-size classes: smaller A. trifasciata were significantly (p < .05) more successful than large A. trifasciata in capturing prey in the 0.50-1.00 size class and even more successful (p < .01) with prey in the smallest relative-size class.

Figure 10.   Success rates for capture of three types of prey offered

in experiments to <u>A</u>. <u>aurantia</u> and <u>A</u>. <u>trifasciata</u>.   Numbers

in parentheses are sample sizes.

DIPTERA

ORTHOPTERA

OTHER ORDERS

A. aurantia
A. trifasciata

% CAPTURED OF NUMBER OFFERED

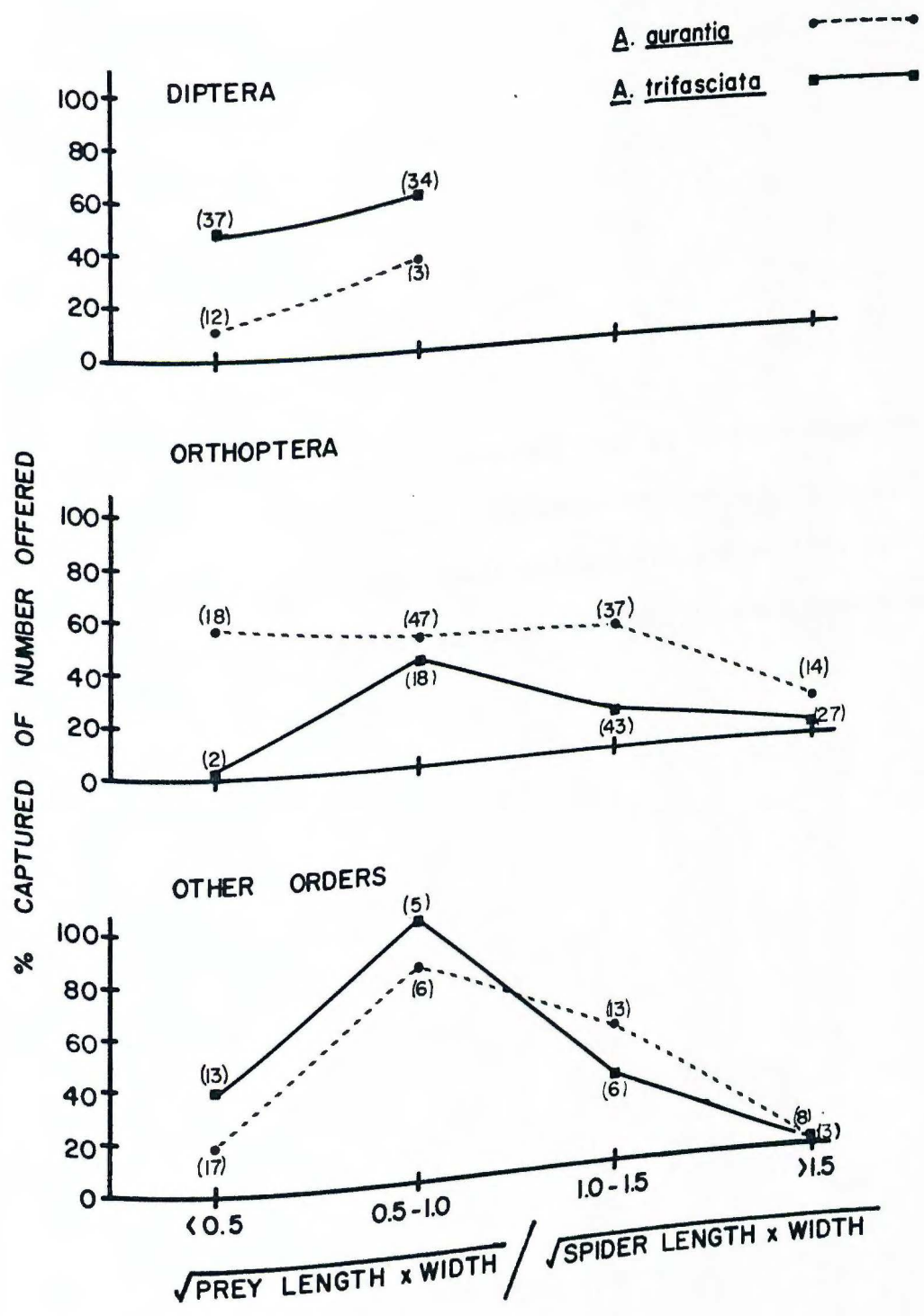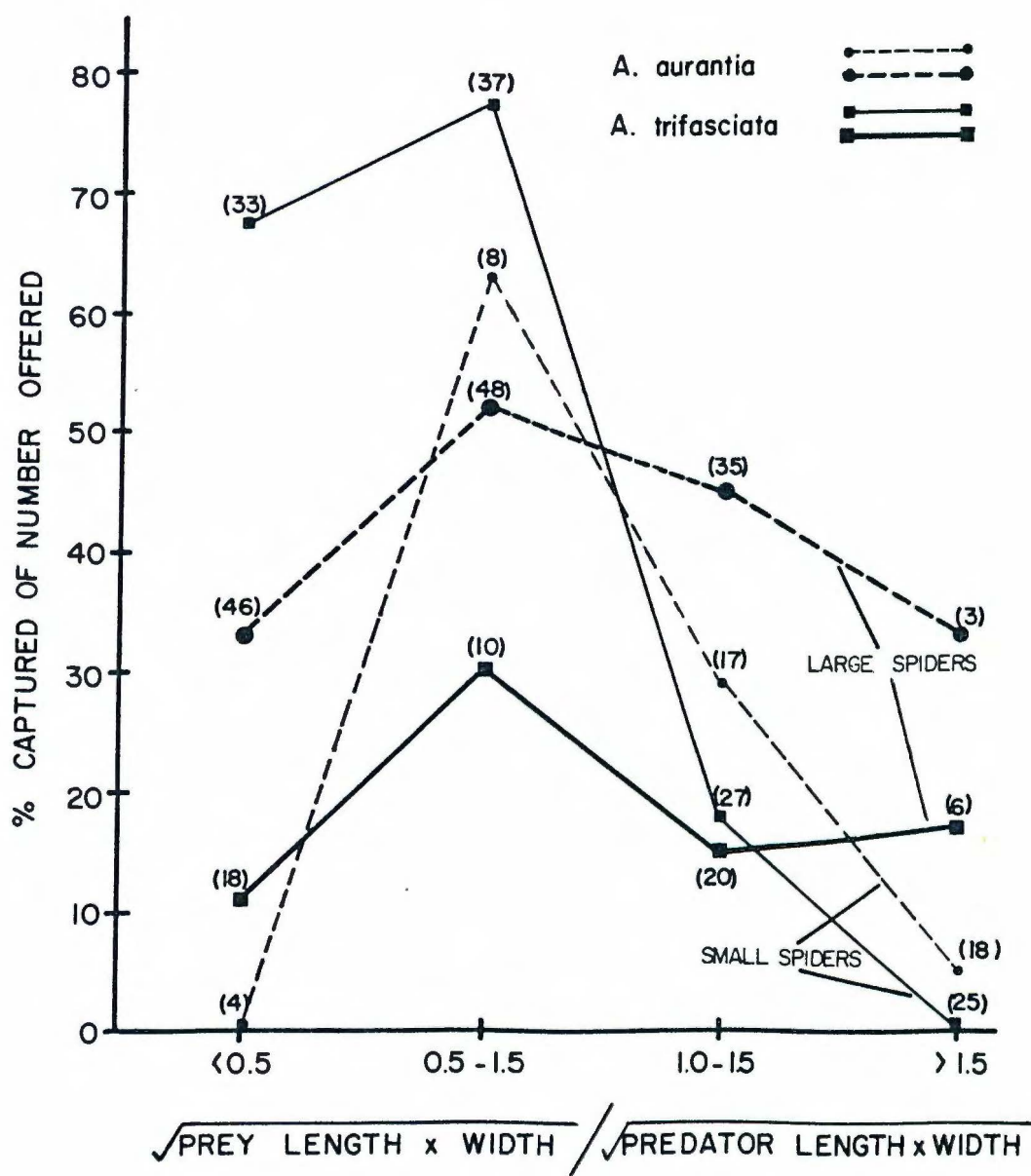√PREY LENGTH x WIDTH / √SPIDER LENGTH x WIDTH

Figure 11. Success rates of capturing prey in various relative-size
classes offered to both large and small A. aurantia and
A. trifasciata. Small spiders are 2-8 mm long and large
spiders are 8-15 mm long. Numbers in parentheses are
sample sizes.

DISCUSSION

Differences in the Size of the Prey

My study indicates that A. aurantia takes larger prey than A. trifasciata (Fig. 2, Appendix 1). The ratio of the difference in the mean food size between these species (d) to the standard deviation in the food size taken by either species (S.D.) is approximately one (d/S.D. = 0.93, 0.94), which is the value proposed by May and MacArthur (1972) for coexisting species.

Differences in the Size of the Predator

Parallel differences in the size of a predator and its prey are often assumed, and the two Argiope species support this assumption, since A. aurantia is, on the average, larger than A. trifasciata (Fig. 1, Appendix 1). Relating difference in predator size to niche separation, Hutchinson (1959) concluded that for two co-occurring, con-generic species to coexist, the approximate ratio of the mean size of their feeding parts should be at least 1.28. The ratio of the cephalo-thorax lengths of A. aurantia to A. trifasciata is 1.35 (Table 1), which exceeds the suggested ratio.

A. aurantia spiderlings emerge from the cocoon several weeks before those of A. trifasciata (Enders 1974; Tolbert pers. comm.). A. aurantia also reach sexual maturity (Bilsing 1920; Comstock 1940) and commence egg laying (Enders 1974); pers. observ.) several weeks earlier than A. trifasciata. Therefore, although they reach approximately the same sizes at similar ontogenic stages, asynchronous breeding cycles insure that the mean spider size of the two species differs at any given point in time.

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Determinants of Size of Captured Prey

Theoretical Explanation

Wilson (1975) suggested that, although the larger of two predators can use food sizes unavailable to the smaller predator, the reverse is often much less true, in that a considerable portion of the diets of some larger predators is made up of small prey. The two Argiope species, however, differ in the proportions of both small and large prey taken (Figs. 3, 4).

The absence of small prey from the diet of the larger predator, which appears physically capable of capturing small prey, can be explained on the basis of optimal feeding theory. According to this theory, small food items are generally less profitable than large food items (Emlen 1966, 1973; MacArthur and Pianka 1966; Schoener 1971). Therefore, predators should take larger food items, but only until the costs of taking larger foods begin to increase faster than the rewards (Emlen 1966, 1973; MacArthur and Pianka 1966; Schoener 1971). Larger predators would be expected to handle larger prey more efficiently than smaller predators; consequently, the optimal food size is expected to be related to the size of the predator (Emlen 1966, 1973; MacArthur and Pianka 1966; Schoener 1971).

How Some Prey Are Excluded

Although optimal foraging theory suggests why some prey should not be part of the spiders' diets, it does not tell how they are excluded. Since a large percentage (63%) of the prey offered experimentally to the spiders were not captured and only a small percentage (4%) escaped after an attempt at capture, spiders and their webs could

exercise considerable influence over the size of prey taken.

Ways of Excluding Prey

Rejection by the Spider

The percentages of the offered prey which adhered to the webs (88%) and were rejected (47%) or successfully attacked (37%) indicate that the spider, rather than the web, appears to be the more important component in determining what size prey is taken (Figs. 8, 9).

Failure of a spider to attack available prey can be a consequence of factors unrelated to the size of the prey. A particular prey item may be rejected because the spider finds it distasteful or dangerous. All prey items may be rejected at times due to the spider's physiological state. Spiders have been reported to be more likely to refuse food before molting (Turnbull 1973) and when they are satiated (Witt et al 1968).

Since very large prey are more likely than small prey to damage the web, injure the spider, or escape after the spider attempts to capture them, they would appear to be more likely than small prey to elicit active rejection. My results bore this prediction out; the percentage of prey actively rejected rose with the relative size of the prey for both A. aurantia and A. trifasciata (Fig. 9C).

Passive rejection appears to involve little or no expenditure of energy and would therefore by a very efficient way of dealing with small prey whose potential reward is small and which are less likely to damage the web or injure the spider than are larger prey. The frequency with which A. aurantia ignored prey increased as the relative size of the prey decreased (Fig. 9D). A. trifasciata did not exhibit

this direct relationship (Fig. 9D). However, at the upper extreme of relative prey size, A. trifasciata's behavior was as expected: they ignored no prey larger than 1.62 X their size. All of the rejected prey soon escaped from the webs and would, in natural situations, be expected to rejoin the pool of available prey.

The Web as a Filter

Some prey pass through the mesh or spaces which exist between strands of a spider's web. If the size of these spaces is related to the spider's size, webs could selectively reduce the availability of relatively small prey. The size of the mesh of spiders' webs, and of A. aurantia's webs in particular, have been found to be a function of the weight of the spiders (Witt and Baum 1960; Reed, Witt and Scarboro 1969). As the spiders' weights increased, so did the mesh dimensions (Witt and Baum 1960; Reed, Witt and Scarboro 1969). On September 24, 1976, not only did I find the width of the mesh of A. aurantia's webs to be larger than that of A. trifasciata, but A. aurantia's web mesh was also relatively larger than that of A. trifasciata (i.e., an A. aurantia equal in size to an A. trifasciata would have a web with wider mesh). Experimental results appear to reflect this difference, since A. aurantia's webs permitted relatively small prey to filter through, whereas A. trifasciata's webs tended to retain them.

Web Adhesiveness

Although prey characteristics other than size influence the like-lihood that prey will stick to webs, one would expect small prey to adhere more frequently than larger prey. Experimental results (Fig. 9A) are in accord with this expectation, for as the size of the prey

increased, relative to the spider whose web was involved, so did the frequency with which it failed to adhere. In general, however, web adhesiveness or the lack of it does not appear to contribute to prey-size differences in the two species of spider.

Ways of Excluding Prey - Summary

The probability of a particular prey item being excluded is influenced by its size relative to the spider, with prey at the extremes of relative size excluded most frequently. Relatively small prey were primarily excluded by both spiders through passive rejection, whereas relatively large prey were primarily excluded through active rejection. For each way of excluding prey which was considered: bouncing off the web, passing through the web, active and passive rejection; A. aurantia eliminated an equal or greater proportion of prey whose prey/spider size ratio was less than 0.50 than did A. trifasciata. A. aurantia's webs allowed some of these prey to filter through, whereas A. trifasciata's webs did not. On the other hand, A. trifasciata captured a smaller percentage of prey whose prey/spider size ratio was greater than 1.0 than did A. aurantia, a difference exhibited mainly between large spiders of both species. Although both species of spider sppear to be selecting prey in the .50-1.0 relative-size range, the mean relative size of prey taken by A. aurantia is larger than that taken by A. trifasciata.

Specialization on Prey Taxa

Another possible mechanism for food partitioning would be for A. aurantia and A. trifasciata to speicalize on different taxa of prey.

However, since spiders prey primarily upon adult insects and as most adult forms are available for only part of the season, specialization on particular prey species is unlikely (Turnbull 1960). The two *Argiope* spiders captured prey from the same orders and in similar proportions, and therefore do not appear to be specializing on different prey (Table 3). Other workers (Bilsing 1920; Turnbull 1960; Riechert and Tracy 1975) have found that spiders attack a diverse taxonomic group of prey dominated by common species.

Vertical Partitioning by Webs

Vertical stratification within the microhabitat is another potential resource partitioning mechanism. It has been proposed that immature *A. aurantia* and *A. trifasciata* partition the microhabitat by constructing their webs at different heights in the vegetation (Enders 1974).

Web Height Differences

In the community which Enders (1974) examined (near Raleigh, North Carolina), *A. aurantia* was the numerically dominant of these two *Argiope* species. From May through July, *A. trifasciata* placed its webs significantly higher than did *A. aurantia* (Enders 1974). In my study area, however, *A. trifasciata* was numerically dominant, and significant differences in the heights at which the two spiders built their webs occurred only in August and September, at which time *A. aurantia*'s webs were higher (Fig. 4).

Dissimilarities between Enders' (1974) study and mine may have been due to differences in the relative and combined abundance of the

two Argiope species in the habitats studied, and in the prey and their distribution within the habitats. The highest Argiope densities reported by Enders (1973) were higher than any I encountered and may account for the prevalence of early-season vertical stratification that he found. If the mean height of vegetation in the area Enders (1974) studied was lower than in the area I studied, this would reduce the possibility of the occurrence of significant differences in web height when webs were at or near their maximum diameter in August and September. Other workers have also observed A. aurantia's webs to be built higher than those of A. trifasciata. Enders (1974) suggested that this may be due to their occurrence in habitats which are less homogeneous than the one he studied. Enders' (1974) paper indicates that his study area was dominated by Lespedeza cuneata and would therefore be more homogeneous than the area I studied.

Population Decline and the Absence of Web Stratification

A high degree of mortality appears to occur during the immature stages of both species. Enders (1974) therefore postulated that the two species could coexist at similar heights in August and September because of the high rate of mortality in the previous months. However, these spiders grow quite rapidly; I found that a decline in population over one month was accompanied by an increase in biomass (Table 3).

Since the size of webs is related to the size of the spider (Witt and Baut 1960; Waldorf 1976), the combined area occupied by webs actually increased.

Prey Stratification

Web stratification can reduce competition for food only if its effect is to increase the amount of prey available to the spiders as a whole. Further, the existence of differences in available prey among strata would, in effect, increase the possibility of partitioning if it coincided with the differences in the species' abilities to use prey. Although the data indicate that the two Argiope spiders are taking the same taxa of prey at the ordinal level, differences in prey taken may nevertheless occur at lower taxonomic levels. Some prey are more likely to be available at one stratum than at another. I collected honeybees (Apis mellifera) from A. aurantia's webs 3 weeks earlier than from A. trifasciata's and found that A. aurantia captured more bees than did A. trifasciata for each week in which honeybees were captured. At that time, the bees were primarily visiting goldenrod. Since the blossoms were at or near the top of these rather tall plants, it is very likely that stratification increased the availability of this resource to the spiders which were able to take advantage of it, thereby increasing the total food supply (i.e., if A. aurantia's webs were not, on the average, higher than those of A. trifasciata, when bees were available, then fewer bees would probably have been caught). Bilsing (1920) also reported that A. aurantia takes more honeybees than A. trifasciata and attributed this to A. aurantia's large size, large webs, and high web placement when wildflowers which attract honeybees started to bloom.

Resource Partitioning - Conclusions

A. aurantia and A. trifasciata thus differ in the mean size of prey they take and in the mean height at which they construct their webs, suggesting that resource separation may be multidimensional. Subtle differences in their habitat preferences have been reported (Bilsing 1920; Gertsch 1949; Levi 1968; Enders 1973, 1974) and may be reflected in web stratification. Alternatively, interspecific aggressive interactions could promote web stratification and may be related to competition for good web sites. Dissimilarities in web stratification between Enders' (1974) study and mine may be related to differences in relative or combined abundance of the two species as well as to possible differences in the particular habitats.

The dissimilarity in mean sizes of prey captured in the experiments resulted primarily from the rejection of a different portion of the available prey by the two species. One might not predict that spiders would reject prey if food were limited in the field; however, Turnbull (1965) found that spiders kept on minimal diets did not attempt to capture all food available to them. Although evidence exists that spiders are generally food-limited (Miyashita 1968; Anderson 1974), rejection rates of 11% and 18% have been reported in desert and woodland-edge habitats, respectively (Turnbull 1960; Riechert and Tracy 1975). The experiments indicate that the prey-capturing abilities of the two Argiope species vary in ways that increase the differences in the sizes of prey that they take. The webs themselves also appear to contribute to the prey-size difference, since relatively small prey of a size which filtered through A. aurantia's webs were retained by A. trifasciata's.

Population Control

The argument presented thus far is consistent with these spiders being controlled in a density-dependent way. However, it is necessary to consider alternative explanations. Predators could alternatively decrease population density and, as Paine (1966) demonstrated, reduce or eliminate competition among their prey. The two _Argiope_ species have well-developed behavioral patterns that act in predator avoidance (flexing the web, dropping off the web, or moving away from the hub: Bristowe 1941; Tolbert 1975), and direct evidence of predation is infrequent. I did not observe any predation upon my spiders. However, Enders (1974) did report occasional predation on immature _A. aurantia_ by non-araneid spiders and psammocharid wasps; and Tolbert (1975) observed encounters between salticid spiders and the two _Argiope_ species in which the salticids were sometimes successful. Predation on _A. aurantia_ eggs, especially by wasps, has been reported (Comstock 1940; Enders 1974); however, the high densities of these spiders early in the season (as many as $12.7/m^2$: Enders 1973) suggests that predation on eggs is unlikely to be controlling these populations. Overall, then, it appears unlikely that predators limited the numbers of the two _Argiope_ species in this study or elsewhere.

Levi (1968) noted a decline in _A. aurantia_ and _A. trifasciata_ populations over several years of drought in New England; however, when rainfall returned to normal in the subsequent year, both species reappeared in large numbers. In fact, in most years these spiders are found to be widespread and abundant in many parts of the United States (Bilsing 1920; Gertsch 1949; Levi 1968; Enders 1973, 1974). Therefore,

little evidence exists to suggest that environmental factors limit these species during most years.

On the other hand, several lines of evidence suggest that the spiders were competing at least during some parts of the study. Although the spider populations studied differ in the mean size of captured prey and in the mean height at which they build their webs, there is some overlap in both parameters. Consequently, prey taken from the range of overlap by one species reduces the food supply of the other. In addition, aggressive interactions between spiders do occur. I observed _A. aurantia_ and _A. trifasciata_ feeding on spiders of their own or the other species. My observations coincide with those of Bilsing (1920) and Enders (1974) in that about 1% of the prey observed on _Argiope_ webs were _Argiope_ spiders. Enders (1974) concluded from the above and other evidence that these spiders invade each other's webs and that interference was probably the proximal cause of their vertical web placement pattern.

The lack of rainfall in the study area during the summer of 1976 may have decreased the prey populations. The smaller size of _A. trifasciata_ on two sampling dates in 1976 compared to the same dates in 1975 could be a direct response to a lower prey population or could, at least partially, result from poor web sites. Sites which were satisfactory in 1975 may have been inadequate in 1976. _A. aurantia_, which built their webs in taller vegetation than did _A. trifasciata_, exhibited no reduction in size. Web sites in tall vegetation should, on the average, be moister than those in shorter vegetation, if only on the basis of the additional shade provided. Janzen and Schoener (1968) and Schoener and Janzen (1968) found that, up to a point, arthropod

abundance increased as one went from dry to moister areas. They also suggested that small arthropods are more susceptible to dessication than are larger ones; a relative advantage for A. aurantia since they take larger prey.

Co-occurring populations of A. aurantia and A. trifasciata often appear to exist at relatively high densities. I found that although density decreased as the season progressed, the rate of individual spider growth and consequent increase in the size of webs is such that a reduction in their populations was, for a time, accompanied by an increase in their total biomass and in the area occupied by their webs. In spite of population decline, web stratification occurred late in the season and was accompanied by the continued and increasing interspecific differences in the size of captured prey. Therefore, while not providing unequivocal evidence, the changes and differences described suggest that the two species were competing for food directly or indirectly by competing for good sites at which to forage.

In general, my study suggests strongly that these two closely related, sympatric species are competing and indicates that they exhibit a variety of differences which tend to reduce the overlap in their use of food and probably reduce the frequency of interspecific interactions. Field data indicate that differences exist in the size of captured prey; and height, site and mesh size of webs. The experiments indicate that they differ in their ability to capture prey of the same relative size.

Appendix 1. Size of spiders, size of prey and height of webs for <u>A</u>. <u>aurantia</u> and <u>A</u>. <u>trifasciata</u>.

Week	Length of spider (mm)					Size of Prey (mm)					Height of Web (cm)				
	A[1]		T[2]			A		T			A		T		
	mean length	n[3]	mean length	n	p[4]	mean $\sqrt{l \times w}$[5]	n	mean $\sqrt{l \times w}$	n	p	mean height	n	mean height	n	p
1975															
28 Aug	18.0	1	12.7	11		6.1	1	3.8	11		80.0	1	60.3	11	
10 Sept	19.9	7	15.6	9	**	6.6	9	4.1	9	*	67.6	7	68.0	9	
23	21.3	4	16.8	9	*	7.2	6	6.8	11		82.0	4	65.2	9	**
30	20.8	5	18.2	20	**	8.0	13	7.8	37		75.4	5	74.3	20	
7 Oct	21.7	3	19.5	14		7.7	4	7.6	16		77.7	3	78.8	14	
14	21.4	5	18.1	11	*	8.6	8	7.0	11		59.8	5	76.4	11	
1976															
14 July	7.5	15	5.8	18	**	2.8	15	2.1	18		33.7	15	36.1	18	
20	8.5	13	6.0	17	**	3.2	16	2.1	18	**	33.8	13	39.6	17	
27	8.7	11	7.0	13	**	3.4	16	2.1	17	**	34.9	11	42.8	13	
3 Aug	9.8	12	7.5	14	**	3.2	15	2.0	16	**	57.0	12	41.4	14	*
11	10.4	15	8.5	13	**	3.5	16	2.4	17	**	53.1	15	50.8	13	
17	12.8	10	8.4	13	**	4.0	15	2.2	15	**	64.1	10	55.4	13	
25	17.1	9	8.9	11	**	5.8	15	3.2	15	**	77.6	9	63.0	11	
3 Sept	18.6	11	10.4	14	**	6.7	18	3.2	15	**	83.4	11	59.2	14	**
10	20.7	9	11.4	14	**	7.8	15	3.4	16	**	75.6	9	54.7	14	**
17	20.3	7	14.7	12	**	8.0	15	5.1	18	**	64.1	7	62.1	12	
24	19.9	8	17.0	9	*	8.7	10	6.3	16	*	66.1	8	63.9	9	

[1]<u>A</u>. <u>aurantia</u>
[2]<u>A</u>. <u>trifasciata</u>
[3]sample size
[4]level of significance, * p <.05, ** p<.01 in F test for ANOVA (spider and prey data ln transformed)
[5] $\sqrt{length \times width}$

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