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THE INFLUENCE OF PREY AVAILABILITY AND HABITAT ON ACTIVITY PATTERNS AND ABUNDANCE OF *ARGIOPE KEYSERLINGI* (ARANEAE: ARANEIDAE)

Richard A. Bradley[1]: School of Biological Sciences, University of Sydney, Sydney NSW, Australia.

ABSTRACT. I examined habitat relationships and prey abundance to determine which (if either) of these factors was more important in determining the local density patterns of the Saint Andrew's Cross spider, *Argiope keyserlingi* Karsch. Focusing on the relationship between a predator and its prey distribution presupposes that prey capture rate is crucial to the biology of the predator. I also studied the influence of prey capture on survival, reproduction and behavior of *A. keyserlingi* as a test of this assumption. Reproduction of females was influenced by food availability under laboratory conditions. Survival was higher among individual females provided with supplemental food in a field experiment. Adult female *A. keyserlingi* moved less frequently when they were provided with supplemental food. Features of vegetation were correlated with patterns of spatial distribution of this spider. There was a highly significant correlation between spider density on the study plots and the density of the understory shrubs that were favored as web sites. On a broad scale, seasonal phenology of activity in *A. keyserlingi* was positively correlated with potential prey abundance. At the scale of individual study plots, there is evidence that prey distribution was unpredictable in both time and space and that neither the activity patterns nor local density of *Argiope keyserlingi* tracked these fluctuations.

Recent experimental studies of arachnid ecology have examined the influence of prey availability and the presence of competitors on the distribution and abundance of these predators (Wise 1979; Greenstone 1978; Schaefer 1978; Horton & Wise 1983; Janetos 1983; Rypstra 1983; Riechert & Cady 1983; Spiller 1984, 1986; Miyashita 1986; Bradley 1989). Of these studies the experimental work of Spiller (1984) provides the only direct evidence of exploitation competition acting on unrestrained spiders in the field.

Riechert & Cady (1983) suggest that interference and intraspecific exploitation competition are more important than interspecific exploitation competition among spiders. For a variety of arachnids interference competition and/or cannibalism influences the number and distribution of individuals (Riechert 1974; Turner & Polis 1979; Riechert & Cady 1983; Wise 1983, 1984; Polis & McCormick 1986a, 1986b; Rubenstein 1987). Despite the paucity of evidence for exploitation competition, several studies have shown that individual arachnids experience shortages of food that limit reproduction (Wise 1975, 1979; Gillespie & Caraco 1987; Morse & Fritz 1982; Fritz & Morse 1985; Suter 1985). These apparently contradictory results may be reconciled if there is no clear density-dependent relationship between arachnids and their prey (Riechert & Lockley 1984). This situation has also been demonstrated in the predatory beetle *Hyphydrus ovatus* L. (Juliano & Lawton 1990).

Wise (1984) suggests that food-limitation does not necessarily imply competition when resources can neither be predicted nor dominated. This situation is possible because individual spiders may encounter insufficient numbers of prey even though prey populations are not regulated by spider density. In contrast, two studies of agroecosystems indicate that spiders do regulate prey populations in these relatively simple environments (Oraze & Gigarick 1989, Riechert & Bishop 1990).

Most arachnids are generalist predators and because prey populations vary unpredictably in both space and time, the foraging success of an individual spider may have little impact on its neighbors. Spiders which capture insufficient prey suffer a "relative shortage of food" (Andrewartha & Birch 1954). Relative shortage occurs when some individuals do not obtain sufficient food yet food is available in the environment. This is often the result of the inability of the predator to locate food, rather than its absence (Andrewartha & Birch 1984). Because polyphagous spi-

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[1] Current Address: Ohio State University, 1465 Mt. Vernon Ave., Marion, Ohio 43302 USA

ders probably do not regulate populations of their prey and live among many other insectivores, Andrewartha & Birch (1984, p. 49) would refer to this situation as a case of extrinsic relative food shortage. Relationships in which the prey (donor) controls predator (recipient) density but not the reverse are referred to as donor-controlled systems (Pimm 1982). I will examine this idea in the context of the omnivorous predator *Argiope keyserlingi.*

It has been shown that habitat structure strongly influences distribution and abundance of orb-web building spiders (Colebourn 1974; Schaefer 1978; Rypstra 1983, 1986) and other arachnids (Riechert 1977, 1979, 1981; Bradley 1986). There is some evidence that suitable foraging or retreat sites may even limit population density and determine the pattern of dispersion of individuals among ground foraging spiders (Riechert 1976) and scorpions (Bradley 1986). Riechert & Gillespie (1986) provided a summary table of the evidence for habitat choice by spiders which indicated that both vegetation structure and prey were important factors, but that very few studies compared these factors. Janetos (1986) suggested that prey encounter rates have a direct impact on web-site occupancy because spiders abandon unproductive sites but also stated that variability of prey encounter at a particular site had been little studied.

The question thus arises, are spider abundance and activity responsive to prey variability, to habitat characteristics, or to some combination of both factors? I examined this question in an empirical study of temporal and spatial relationships between a generalist predator, the orb-weaving spider *Argiope keyserlingi* Karsch, and its habitat and arthropod prey. My study had two primary goals: 1) to assess the importance of variation in prey availability on activity patterns of *A. keyserlingi* and 2) to compare the relative influence of prey abundance and habitat features on the pattern of local distribution of *A. keyserlingi* individuals. A central assumption of community ecology has been that the abundance of food resources is crucial in determining patterns of predator distribution and abundance (Wiens 1989, p. 16). In this study I tested the assumption that food availability is important to *A. keyserlingi* by assessing the influence of foraging success on survival and reproduction in female *A. keyserlingi.*

Argiope keyserlingi is common in a variety of habitats along the east coast of Australia from NE Queensland south to NE Victoria. In Australia this spider is commonly but incorrectly known as *A. aetheria* (Levi 1983). It builds orb webs in low vegetation in open habitats, including heathland and salt marsh, as well as the understory of evergreen sclerophyl woodlands and forests. In the Hawkesbury Sandstone plateau of New South Wales they seem most abundant in the understory of dry open forest (Benson & Fallding 1981). This study focused on one open forest population of this species. After emergence from the egg case, second-instar *A. keyserlingi* disperse (often by ballooning). Fresh egg cases collected in the field and kept in the laboratory hatched 14–25 days after they were laid ($\bar{x} = 19$, SEM = 1.4, $n = 9$). Juveniles build their first webs in late summer (February and March). They over-winter as immatures and emerge in spring (November). Data from spider censuses on the study area indicate a brief synchronous activity period (Fig. 1A). In addition to these census data, qualitative observations for the previous (1983/84) and subsequent (1986/87) summers conform to the same restricted activity period. Individuals found in other habitats of the Sydney region are active for much longer periods during the year. Adult female *A. keyserlingi* usually die after laying eggs, and I often found their carcasses hanging in or lying on the ground below the web in January and February. A few *A. keyserlingi* females survive the winter and become active again during the following spring. These females may either represent late-maturing or truly biennial individuals.

METHODS

General methods.—The study site was located in Brisbane Water National Park, near the University of Sydney's Crommelin Biological Research Station at Pearl Beach NSW (33° 33′ S, 151° 18′ E). The habitat is dominated by *Casuarina torulosa* Ait. (70% of trees), *Angophora costata* (Gaertn.) J. Britt, *Eucalyptus* spp. and *Syncarpia glomulifera* (Sm.) Niedenzu. The understory is relatively open, with many shrubs, principally *Xanthorrhoea resinosa* Pers., *Dodonaea triquetra* Wendl., *Livistona australis* (R. Br.) Mart., and *Lasiopetalum ferrugineum* Sm. The site is on a north-facing hillside with a few exposed rock outcrops and a dense mat of *Casuarina* litter (5–20 cm deep). Sixteen 0.023 ha (15 m × 15 m) square sampling plots were established and marked with wooden stakes. The plots were separated by a minimum of 5 m.

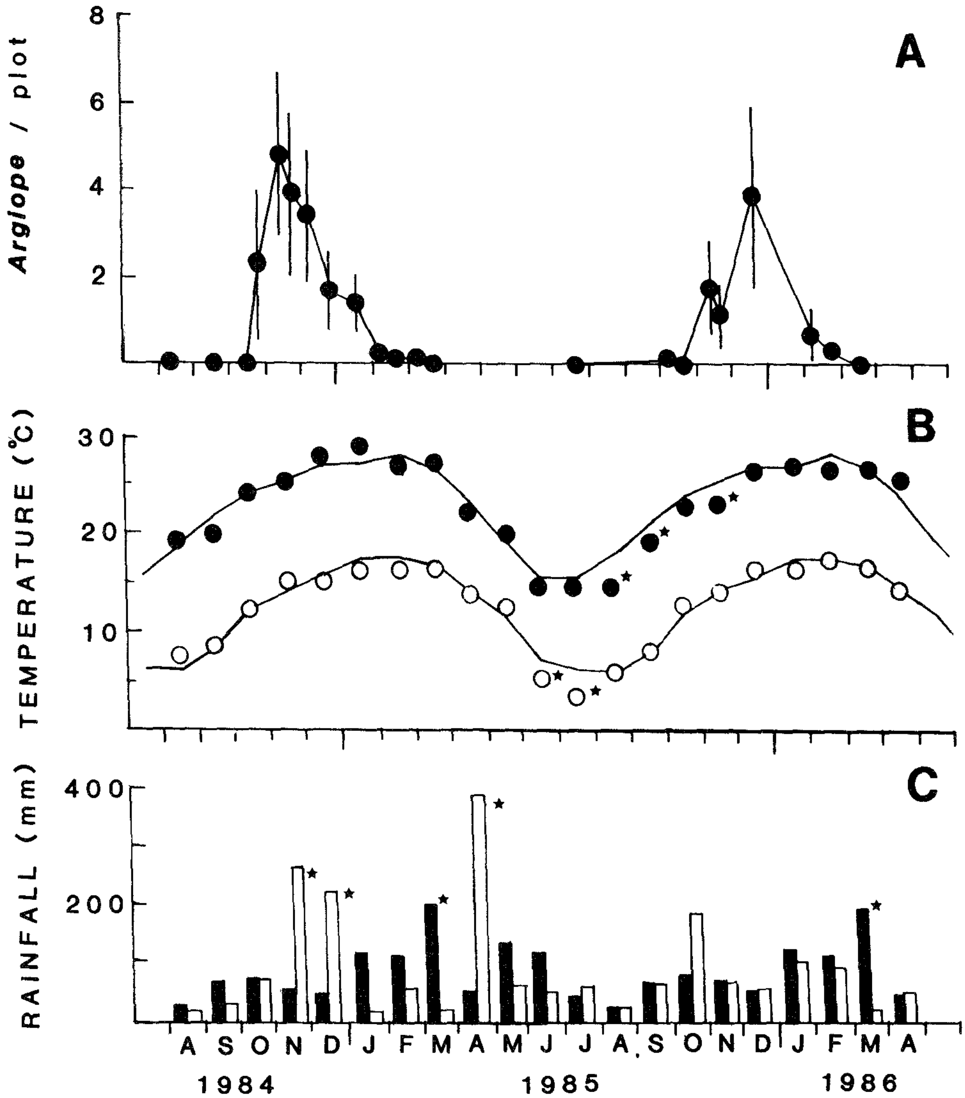

Figure 1.—Activity phenology and weather statistics for *Argiope keyserlingi* during the 1984/85 and 1985/86 seasons. **A.** *Argiope* activity in mean number of spiders per plot ($n = 16$) for each sampling date. The vertical bars indicate the 95% confidence limits on this mean. **B.** Mean monthly temperature at the study area (°C). The solid dots are the mean high temperatures for the sampling month, and the open dots are the mean low temperatures for the sampling month. The lines connect the normal mean high temperature and normal mean low temperature patterns based on the previous 10 years of weather records ($n = 3647$ sample dates). Stars indicate monthly averages that differ from the 10-year average (z-test, $P < 0.05$). **C.** Monthly rainfall in mm, the solid bars are means based on the previous 10 years of weather records, the open bars are the actual rainfall totals for the sampling month. Stars indicate rainfall values that differ from the 10-year average (z-test, $P < 0.05$).

The number, DBH (diameter at breast height) and identity of all trees and the number of perennial shrubs were counted for each study plot. Twelve summary habitat variables (Table 1) were subjected to principal components analysis. The principal component scores for each plot along the first three axes were compared to measures of spider density using the Pearson product-moment correlation (r_p). Mean elevation was calculated for each plot. Features of the perennial vegetation changed little during this study and were measured only once (spring 1986). Three descriptive variables (top thread length, sticky orb diameter, and height above ground at orb

Table 1.—*Argiope keyserlingi* density and habitat features on the 16 study plots. Variables: *Argiope* = $\bar{x}$ no. spiders/plot, Ang# = no. of *Angophora costata* and *A. floribunda,* Euc# = no. of trees in genus *Eucalyptus* (8 species), Cas# = no. of *Casuarina torulosa,* Bank# = no. of *Banksia serrata,* Syn# = no. of *Syncarpia glomulifera,* Totlg = total no. of trees, Diam = $\bar{x}$ diameter of trees (breast height), Totar = cross-sectional area of trees at breast height (m^2), Xanth = no. of *Xanthorrhoea resinosa,* Macz = no. of *Macrozamia communis,* Palm = no. of *Livistona australis,* Totsm = total no. of small shrubs, Totvg = Totlg + Totsm, Elev = $\bar{x}$ elevation of plot (m).

	Argiope numbers ($\bar{x}$ spiders/plot)		Habitat features													
			Trees & large shrubs								Small shrubs					
Plot #	84/85	85/86	Ang- #	Euc- #	Cas- #	Bank- #	Syn- #	Totlg	Diam	Totar	Xanth	Macz	Palm	Tot- sm	Totvg	Elev
1	7.5	3.7	0	2	11	9	0	22	18.2	0.85	7	3	31	41	63	35.1
2	10.8	8.3	0	3	32	0	0	35	19.0	1.61	25	4	30	59	94	35.1
3	4.0	0.3	1	1	24	3	0	30	17.0	1.13	2	0	24	26	56	36.3
4	4.0	5.0	2	2	26	3	0	32	15.6	1.47	6	2	9	17	49	36.3
5	4.3	3.7	1	7	3	5	0	11	21.0	1.37	4	1	6	11	22	37.5
6	2.3	1.3	6	0	5	2	0	21	12.1	0.31	3	0	0	3	24	37.5
7	1.0	0.0	0	8	29	1	2	32	11.0	0.40	3	0	1	4	36	41.5
8	1.5	2.0	0	3	12	2	7	29	16.7	0.95	1	0	0	1	30	37.5
9	1.5	2.0	0	4	24	0	0	27	18.8	1.03	0	0	17	17	44	37.5
10	2.0	0.7	0	4	37	1	5	47	14.0	1.03	0	1	4	5	52	37.8
11	2.3	1.3	0	0	35	0	3	38	13.7	0.68	2	0	2	4	42	38.7
12	5.3	1.7	0	6	41	0	5	52	13.8	1.04	4	1	6	11	63	37.5
13	3.0	1.7	1	2	27	1	9	40	15.3	1.39	0	7	46	53	93	37.2
14	3.3	1.7	2	8	15	3	8	36	14.3	0.81	1	4	9	14	50	36.9
15	1.0	0.3	1	17	14	0	0	32	13.8	0.67	0	0	1	1	27	38.4
16	1.5	2.0	0	4	21	1	0	26	13.2	0.47	0	2	13	15	47	36.3

center) were measured on 118 webs of *A. keyserlingi* mature females and 57 webs of immature females (total body length [tbl] < 7 mm). Total body length [tbl] was measured from the anterior end of the median ocular area to the tip of the opisthosoma. Mature male *Argiope keyserlingi* often inhabit the webs of females, and may act as kleptoparasites as they do in other species (Robinson & Robinson 1978; Suter 1985). Occasionally males are found in small webs alone; 15 such webs were measured and attributed to males. A sample of 26 *A. keyserlingi* egg cases was collected from areas adjacent to the main study area during early February 1985. These cases were weighed to the nearest 0.1 mg (Mettler balance), dissected and the number of eggs counted. A second sample of 19 egg cases collected in late February 1985 was weighed and maintained in the laboratory until the spiderlings emerged, and these were counted.

Spider censuses.—Visual censuses were conducted early in the morning on each of 14 dates between August and March 1984/85 and 9 dates between July and March 1985/86. Each plot was censused by walking slowly and looking in and under vegetation to detect *Argiope* webs. Repeat censuses were conducted by a second observer for the first two dates to verify the efficacy of the method. Each spider found was classified into one of 3 length categories (0–5 mm tbl, >5–7 mm tbl, >7 mm tbl).

Prey abundance.—Potential prey abundance was assessed using sticky-boards. Brown Masonite© boards 25.5 cm × 30.0 cm were placed on wood posts with the center of the board 1.2 m above the ground surface. The size of a sticky-board is similar to that of an adult *Argiope* web. Prey samples were collected once per month for each month when spiders were active (September—February). The sample for October 1985 was lost. On each sampling date a clear tight-fitting plastic bag was slipped over the board and both sides of the bag were coated with Tanglefoot© insect trapping adhesive. The plastic bag covered with Tanglefoot reflected the colors of the surrounding vegetation. Four boards were used on each of the 16 plots, with two oriented in a N–S direction and two oriented in an E–W direction. On each sampling date the bags were left out for 24 h. To collect the bags, a larger plastic bag was inverted over the sticky-bag and both were removed. This left a clear plastic coating over the specimens, and all subsequent identifications and measurements were made through the plastic. These traps were used because they were successful in pre-sampling tests at capturing examples of the known prey items in the diet of *Argiope keyserlingi* (see below). Because sticky traps do not behave like spiders (Robinson & Robinson 1973; Rypstra 1982; Castillo & Eberhard 1983), I treated these data as an index of prey abundance rather than a measure of actual prey availability.

Each arthropod captured on the sticky-boards was measured to the nearest 1 mm (body length). Dry-weight biomass was estimated using regression equations appropriate for each taxon (Rogers et al. 1976, 1977). In cases where no appropriate regression equation was available, I calculated one from specimens captured in the study area. Any arthropods that were captured on the sticky traps which were not taken by *Argiope keyserlingi* when fed to spiders in the laboratory were eliminated from the sample. Most insects were identified to the ordinal level; large insects (> 10 mm body length) were identified to the family level. Three summary variables were tabulated for each sample of potential prey; 1) total number (NUMB), 2) number of large prey [> 5 mm body length, NBIGS], and 3) total biomass (BIOM). Analysis of spatial and temporal patterns of these potential prey variables were analyzed using a randomization test (Sokal & Rohlf 1981). A randomization test (repeated-measures ANOVA) was used because these data violated assumptions of traditional ANOVA (normality, heteroscedasticity) even after transformation. The randomization test (F-ratio used as test statistic) provided a robust, ANOVA-based way to examine variation among dates and across plots. A model that incorporated the repeated measures (boards on plots, dates) was used in the randomization-ANOVA. The SAS GLM (SAS 1988) procedure was used to calculate the SSQ values. A SAS data statement procedure was written to conduct the random re-assignments. Actual values were compared to 1000 randomized trials for estimation of significance. Parametric ANOVA (SAS GLM) was applied to web-characteristic data because these data met requisite assumptions. Correlation analyses were conducted to compare both temporal and spatial variation in the prey variables to spider census data. All data were tested for normality using the SAS univariate procedure. Pearson's product-moment correlation coefficient (r_p) was used when data met parametric assumptions. Spearman Rank correlation (R_s) was applied where data were not normally distributed. Autocorrelation with a lag of 1 was used to assess temporal variation in the spatial patterns of prey distribution. For this test the data for all four sticky boards were combined to produce one mean value of each prey variable for each date/plot combination.

Prey captured by *A. keyserlingi* in the field were also identified and measured. The frequency distribution of insects taken from *Argiope* webs was compared to that collected on the sticky-boards for both size and taxonomic grouping using a χ^2 goodness-of-fit test.

Stepwise multiple regression.—I compared the relative importance of vegetation and prey as independent variables for their ability to explain variation in *A. keyserlingi* density. The mean values of six habitat variables (number of *Xanthorrhoea*, number of *Macrozamia*, number of *Livistona*, number of large shrubs, plot elevation and the first Principal Component Score for each plot) and mean values of three prey variables from the sticky board sampling (NUMB, BIOM, NBIGS) were compared to the dependent variable *A. keyserlingi* density across the 16 sampling plots. The analysis was done separately for each of the two years of this study. While the distribution of individual variates for these variables was skewed (see above), the mean values used in this analysis were approximately normally distributed (Shapiro-Wilk statistic, $P > 0.05$), and their variances were homogenous (Bartlett-Box F and Cochran's C tests $P > 0.05$). I used SAS REG procedure for these analyses, with the forward selection option (SAS 1988).

Laboratory experiment.—I captured 29 female *A. keyserlingi* (penultimate instar) near the Crommelin Biological Research Station on 10 November 1984. These spiders were weighed to the nearest 0.1 mg on a Mettler balance and introduced into individual (30 × 30 × 7 cm) clear perspex (Plexiglass) containers. Two wood dowels were fixed vertically in each container with a piece of cotton thread strung between them about 2 cm from the top of the container. The spiders readily built orb webs parallel to the long axis of the containers, usually within hours of installation. A ball of moist cotton (re-wetted daily) was placed in each container to maintain humidity. Each container had a 10 × 10 cm door on the center of one side for feeding. After the spider had constructed a web, this door could be opened and potential prey placed in the web. Any prey that was not consumed was removed after 24 h. The spiders were randomly divided into two groups. One group (low food) was fed 1 adult *D. tryoni* once every other day ($\bar{x}$ = 12 mg/feeding, SEM = 0.1 mg, n = 79). The second group (high food) was fed 4 adult Queensland fruit flies (*Dacus tryoni* (Froggatt)) once every other day ($\bar{x}$ = 48 mg/feeding). For comparison, the median biomass of prey captured on one sticky-board is 11.6 mg/day (no comparative data for captures in the natural webs of *A. keyserlingi* are available). After a female molted into the final instar, a freshly-captured adult male *A. keyserlingi* with fully expanded palps was introduced to the container. Any egg sacs were removed and weighed, and the number of eggs counted. Females that died during the experiment were removed and weighed as soon as they were discovered (usually within 12 h). At the end of the experiment (25 February 1985) the surviving females were removed and weighed.

Field experiment.—A food manipulation experiment was conducted to investigate the influence of supplemental prey on the behavior, survival and reproduction of adult female *A. keyserlingi*. On 10 December 1985, 80 adult female *A. keyserlingi* were located and their webs were mapped and marked in a corner with inconspicuous paper tags. The spiders were randomly divided into four groups: fed and marked (n = 30), fed and unmarked (n = 10), unfed and marked (n = 30), and unfed and unmarked (n = 10). The unmarked spiders in both treatment groups were included as a control for the marking procedure.

Spiders in the fed group were supplied with one meal worm (*Tenebrio molitor* Linnaeus) larva ($\bar{x}$ = 0.16 g, SEM = 0.01 g, n = 19) twice per day for four days. The web was watched until the spider had captured and wrapped the supplemental prey to confirm that prey did not escape. Spiders that were to be marked were captured in a plastic vial and anesthetized with CO^2 gas. They were then marked with four colored non-toxic paint dots in a unique combination. I judged that the small paint dots did not increase the conspicuousness of these brightly colored spiders. The spider was then released back onto its web. All spiders were found each day and if they had moved their new position was mapped and marked. A team of four observers was used to search for spiders. Spiders that disappeared were scored as missing. Any marked spiders that molted (but remained in the same web) were remarked. Freshly molted *A. keyserlingi* were easily recognizable. Female *A. keyserlingi* are quiescent at the time of molting and marked exuviae were found below the freshly molted individuals. Nevertheless, some individuals may have moved and molted, and these would have been scored as missing. Such movement was relatively rare in *Argiope trifasciata* Forskal and *A. aurantia* Lucas and the rate increased after molting (Enders 1975). Although web-invasion was possible (Riechert & Gillespie 1986; Hoffmaster 1986), many web movements of marked spiders were observed and no marked spiders were ever relocated in a web site that was previously occupied by another marked individual. The experiment was divided into three periods: pre-treatment period (4 d; 10–13 December), treatment period (4 d; 14–17 December), post-treatment (5 d; 18–22 December). G-tests of independence (2 × 2; Model II) were used to evaluate movement/mortality data from this experiment (Sokal & Rohlf 1981). Individuals were checked on seven subsequent dates (4 Jan to 10 March) and any egg cases that were found in marked webs were collected. These cases were maintained in the laboratory and the number of spiderlings which emerged from these cases was counted.

RESULTS

Natural reproduction.—I detected significant variation in reproductive output among individual female *Argiope* in the field. This was expressed by increasing the clutch size rather than egg size. Egg cases from 26 natural (no food supplementation) female *A. keyserlingi* had a mean mass of 0.095 g (SEM = 0.01 g), equivalent to 44% of a female's mass before laying ($\bar{x}$ = 0.21 g, SEM = 0.02 g, n = 29). These egg cases contained 4–750 ($\bar{x}$ = 298, SEM = 46, n = 26) eggs. For a second sample of 19 egg-cases, mass was strongly correlated with the number of juveniles that emerged (r_p = 0.99, $P < 0.001$). Thus the variation in egg case mass is almost completely explained by variation in numbers of eggs; variation in egg size is relatively unimportant. Females laid from 1–4 egg cases; the maximum reproductive output for any single unmanipu-

Table 2.—Web characteristics of *Argiope keyserlingi*. Mean ($\bar{x}$), standard error of the mean (SEM), 95% confidence interval about the mean (conf. int.).

Age/sex class	n	Top thread length (mm) and $\bar{x}$ (SEM, conf. int.)	Orb diameter (mm) and $\bar{x}$ (SEM, conf. int.)	Orb height (mm) and $\bar{x}$ (SEM, conf. int.)
Immature female	57	201 (14, 173–229)	118 (8, 101–134)	737 (40, 656–818)
Mature female	118	278 (12, 255–301)	185 (7, 172–199)	809 (34, 741–876)
Mature male	15	129 (29, 66–192)	65 (21, 20–111)	793 (101, 576–1009)
Classes combined	190	243 (8, 225–261)	155 (11, 143–167)	786 (25, 736–836)

lated female was 850 spiderlings (from 3 cases; 207, 258, 385).

Natural webs and prey.—Some web characteristics differed among the age/sex classes of *A. keyserlingi* (Table 2). Webs of mature females were significantly larger than those of immature females (top thread length ANOVA $P < 0.001$, orb diameter ANOVA $P < 0.001$). Webs of mature males were significantly smaller than either class of females (ANOVA $P < 0.001$). This is not surprising considering the fact that males of this species are tiny (mean mass = 0.005 g, SEM 0.001 g, $n = 15$) and rarely feed. The sticky orbs of all classes were at similar heights (ANOVA, *ns*).

The mean mass of 31 natural prey items was 0.04 g (SEM = 0.01 g), ranging from small gnats and mosquitos (<0.001 g) to a large predatory fly (Diptera: Asilidae, 0.12 g). The size distribution (six categories) of these prey was compared to that of potential prey captured on the sticky boards ($n = 1783$, Fig. 2). The spiders captured significantly more large prey ($\chi^2 = 365$; $df = 5$; $P < 0.001$). Large prey (>0.05 g) constituted 26% of *Argiope* prey but only 0.9% of potentially available insects. Prey were also compared to taxonomic assignment (by order, 10 categories); significantly fewer flies (all Diptera combined) and more wasps (Hymenoptera combined) were captured by the *Argiope* than the sticky boards ($\chi^2 = 254$; $df = 9$; $P < 0.001$). Flies made up 19% of *A. keyserlingi* prey but 81% of potential prey. Hymenoptera made up 29% of *Argiope* prey but only 4% of potential insect prey.

Spider density.—I calculated density for both 1984/85 and 1985/86 on each of the 16 study plots. This estimate is based on the mean number of spiders/plot for all censuses when spiders were active. The mean density in 1984/85 was 150 spiders/ha (SEM = 29, $n = 16$) and in 1985/86 it was 97 spiders/ha (SEM = 24, $n = 16$). There was considerable variation across the 16 study plots; 1984/85 coefficient of variation (CV) = 76%, 1985/86 CV 94% (Table 1). Density patterns across plots were consistent between years ($r_p = +0.81$; $P < 0.01$).

Argiope keyserlingi density was not related to any of the tree or large shrub variables, although it was significantly correlated with total numbers of small shrubs (1984 $r_p = +0.74$, $P < 0.001$; 1985 $r_p = +0.62$, $P < 0.01$). This relationship is primarily due to a strong correlation with *Xanthorrhoea resinosa* numbers (1984 $r_p = +0.88$, $P < 0.001$; 1985 $r_p = +0.86$, $P < 0.001$). *Xanthorrhoea* plants are a favored web site for *Argiope*. Principal component analysis generally

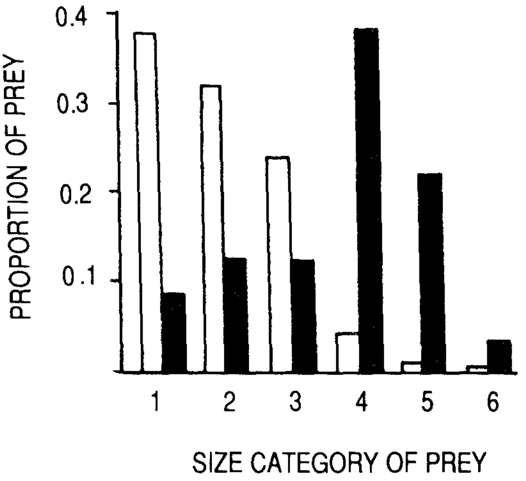

Figure 2.—Relative proportions of prey in six biomass categories. The vertical scale is the percentage of the sample which belongs in the size category. The six categories (horizontal scale) are: 1. 0–0.001 g; 2. >0.001–0.005 g; 3. >0.005–0.01 g; 4. >0.01–0.05 g; 5. >0.05–0.1 g; 6. > 0.1 g. The open bars represent the proportions of potential prey in the sticky-board samples ($n = 1783$), the solid bars represent the proportions of prey captured and consumed by *Argiope keyserlingi* observed in the field ($n = 31$).

Table 3.—Results of autocorrelation analysis for prey sampling variables. The values in the body of the table are the mean correlation for lag = 1 among all dates (1984/1985 $n = 5$, 1985/1986 $n = 4$). None of the individual correlation or mean correlation values are statistically significant. Large prey have a total body length >5 mm.

Year	Numbers	Number large prey	Biomass
1984/1985	−0.04	+0.002	+0.08
1985/1986	+0.07	+0.08	+0.04

failed to clarify the relationship between vegetation and spider density. *A. keyserlingi* density was correlated with principal component axis 3 of the vegetation analysis (1984 $r_p = +0.69$, $P < 0.01$; 1985 $r_p = +0.71$, $P < 0.01$). This axis was positively weighted on numbers of larger broadleaf trees (higher canopy) and *Macrozamia* density, both factors are indicative of a mesic microenvironment. This axis, however, explains only about 12% of the variation in the vegetation data. Neither the first nor second principal component axis was significantly correlated to spider density. Spider density was negatively correlated with plot elevation (1984 $r_p = -0.67$, $P < 0.01$; 1985 $r_p = -0.65$, $P < 0.01$). This feature covaried with vegetation characteristics, probably because the lower plots were nearer a small creek and supported lush shrub growth.

Relationship to prey.— *Temporal patterns*: Appearance of foraging spiders on the study area was slightly delayed during the spring of 1985/86, possibly due to an unusually cool fall (Fig. 1B). Despite this, the date of first appearance and general phenology of *Argiope* during the four summers from 1983/84 through 1986/87 were all quite similar despite unusual patterns of rainfall. There was a drought prior to the summer of 1983/84 and unusually heavy rains during the spring (November and December) of 1984 (Fig. 1C).

Seasonal abundance patterns of potential prey, as revealed by the sticky board samples (NUMB, NBIGS), exhibited significant variation among sampling dates (Repeated-measures ANOVA randomization test $P < 0.001$). This seasonal pattern of variation was consistent for corresponding sampling dates during the activity period of *A keyserlingi* between years (NUMB $R_s = +0.90$, NBIGS $R_s = +0.80$). Although the pattern of seasonal variation in potential prey biomass (BIOM) was also significant (Repeated-measures ANOVA randomization test $P < 0.001$), it was not consistent between years (BIOM $R_s = -0.40$, Fig. 3). The pattern of *A keyserlingi* seasonal abundance (averaged across plots) was positively correlated with all three prey variables for 1984/85 (NUMB $R_s = +0.90$, BIOM $R_s = +0.60$, NBIGS $R_s = +0.50$). This comparison for the 1985/86 season revealed a positive correlation between spider and prey numbers (NUMB $R_s = +0.90$, NBIGS $R_s = +1.0$), but not between spider numbers and prey biomass (BIOM $R_s = -0.10$). Overall, the general seasonal phenology of *A. keyserlingi* was related to the seasonal pattern of abundance of potential prey.

Relationship to prey.—*Spatial patterns*: Spatial patterns of distribution of potential prey numbers (NUMB, NBIGS) across the 16 study plots exhibited significant variation (Repeated-measures ANOVA randomization test $P < 0.05$). Spatial variation in biomass (BIOM) across plots was not significant (Repeated-measures ANOVA randomization test $P = 0.08$). The spatial patterns were not consistent between years (NUMB $R_s = +0.26$, BIOM $R_s = -0.26$, NBIGS $R_s = +0.16$; all *ns*). Autocorrelation of the three prey variables using a lag of 1 (comparing a month with the preceding month) with the 16 plots as replicates, detected no significant correlations (Table 3). Thus the spatial patterns of variation in prey across plots were not even consistent from month to month (Fig. 3). As concluded above *A. keyserlingi* density on the plots was very consistent, and it is therefore not surprising that there was no relationship between *A. keyserlingi* on the plots and any of the potential prey variables when all dates are combined. A correlation ma-

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Figure 3.—Summary of biomass of potential prey captured on sticky boards during the two sampling years (1984/1985, 1985/1986). Each dot represents the mean biomass captured on the four sticky boards on that plot for that sampling date (horizontal scale). The vertical scale is biomass in mg plotted on a log scale. The 16 graphs correspond to the 16 field sampling plots. Note that there is no consistent pattern across dates or plots, and that no plot had consistently high or low potential prey captures.

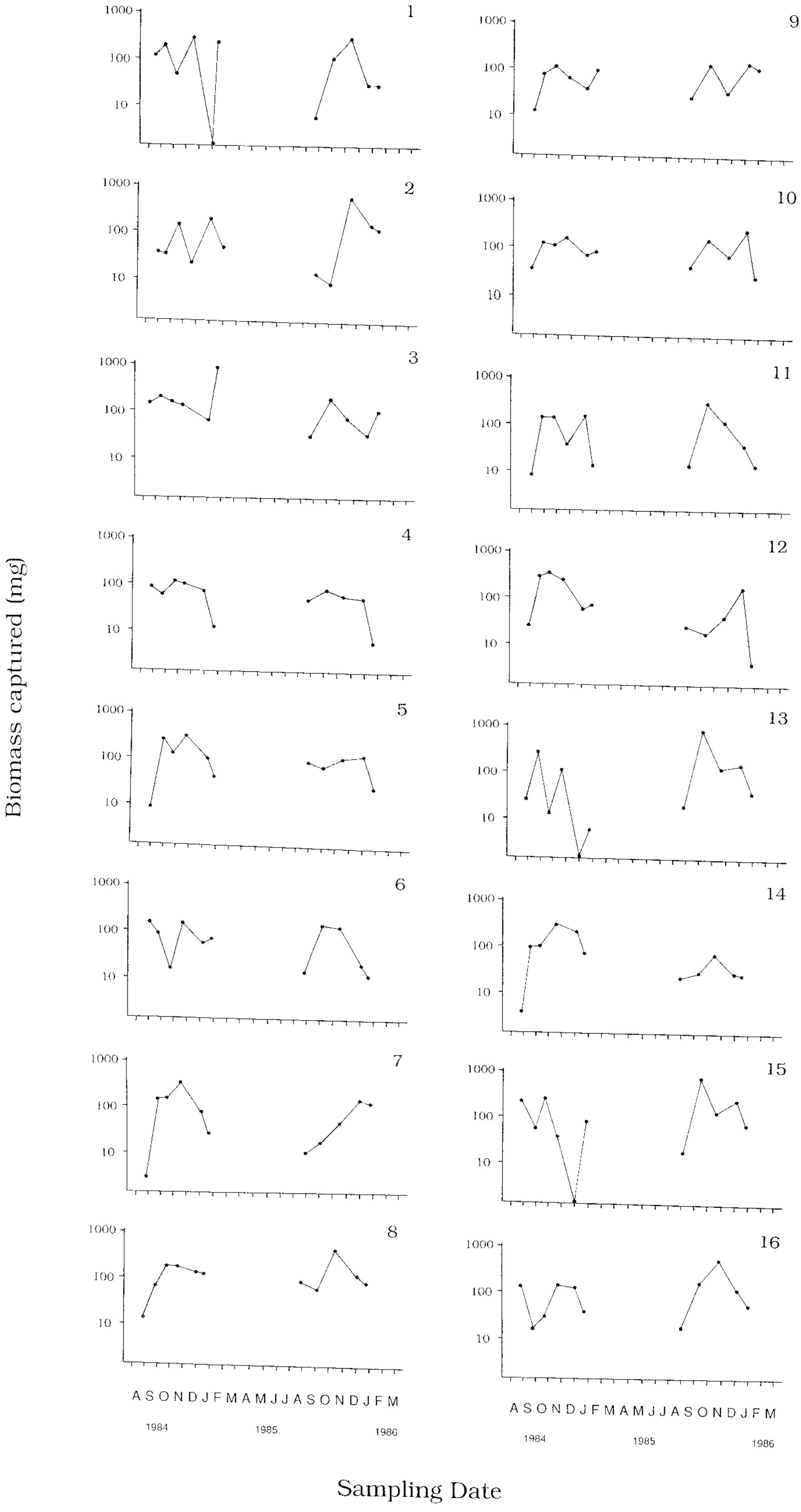
Biomass captured (mg)
1000
100
10
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
A S O N D J F M A M J J A S O N D J F M
1984
1985
1986
Sampling Date

Table 4.—Results of stepwise multiple correlation analysis of habitat and prey variables against the density of *Argiope keyserlingi* for the two study years.

Variable entering model	Partial r^2	Cumulative r^2	Significance $P <$
1984/1985 season			
Xanthorrhoea density	0.77	0.77	0.0001
Plot elevation	0.10	0.87	0.01
Prey biomass	0.05	0.92	0.05
Macrozamia density	0.02	0.94	*ns*
1985/1986 season			
Xanthorrhoea density	0.75	0.75	0.0001
Plot elevation	0.08	0.83	0.05
Total large shrub density	0.01	0.84	*ns*
Macrozamia density	0.01	0.85	*ns*

trix between spider density and potential prey variables for all date and plot samples (data not combined for rows or columns, thus all combinations calculated separately) revealed no significant correlations.

Stepwise regression analysis.—This analysis simultaneously compares the relationships between habitat and potential prey patterns and their correlation with variation in *A. keyserlingi* numbers on the study plots. The analysis revealed that habitat features were far more important predictors of spider distribution (Table 4). For both years the number of *Xanthorrhoea* entered the model first, this factor alone explained 77% and 75% of the variation in spider density for 1984/85 and 1985/86. Again for both years plot elevation was the next factor to enter explaining an additional 10% and 8% of the variation in spider numbers. All three of the potential prey measures combined explained only 6.7% of the variation in spider density in 1984/85 and <1% in 1985/86. The clear conclusion from this analysis is that habitat characteristics were a better predictor of spider density than measures of potential prey on the same plots.

Laboratory experiment.—All laboratory females mated with the males presented to them. Females maintained under the high-food treatment increased by an average of 49% of their initial mass, while those maintained under the low-food treatment did not significantly change in mass (Table 5). Of the 15 high-food treatment females, 12 produced egg cases; these females had a total reproductive output similar to that measured in the field (Table 5; *t*-test, *ns*). Only 7 of 14 females maintained under the low-food treatment produced egg cases. These females had a reproductive output significantly lower than the high-food treatment group (Table 5; *t*-test, $P < 0.05$).

Field experiment.—There were no differences in web-site movement or disappearance of marked and unmarked females, so these two categories were combined for subsequent analyses. There were no differences in the proportion of females moving between the fed and unfed groups during the pre-feeding (control) period. Significantly fewer females supplied with supplementary food moved during the feeding and post-feeding periods (G-test, $P < 0.001$; Fig. 4). Of those females that moved, there was no difference in distance moved between treatment groups (combined $\bar{x}$ = 1.3 m, SEM = 0.2 m, n = 65).

There was no significant difference between survival (as estimated by the disappearance of individuals) of the fed and unfed groups during the pre-feeding (control) period. There was a difference in the proportion missing during the feeding period: more unfed individuals van-

Table 5.—Reproduction of *Argiope keyserlingi* in the laboratory and field. The "high food" treatment averaged 48 mg/feeding and the "low food" group averaged 12 mg/feeding. A sample of females observed in the field is included for comparison. For these females the number of juveniles was estimated (=number eggs counted).

Treatment group	n	$\bar{x}$ change in mass (SEM)	$\bar{x}$ number of egg cases per female	Total number of juveniles emerged per female (SEM)
High food	15	+0.103 (0.04)	1.2	293 (57)
Low food	14	−0.031 (0.01)	0.6	120 (39)
Field	26	no data	1.4	367 (46)

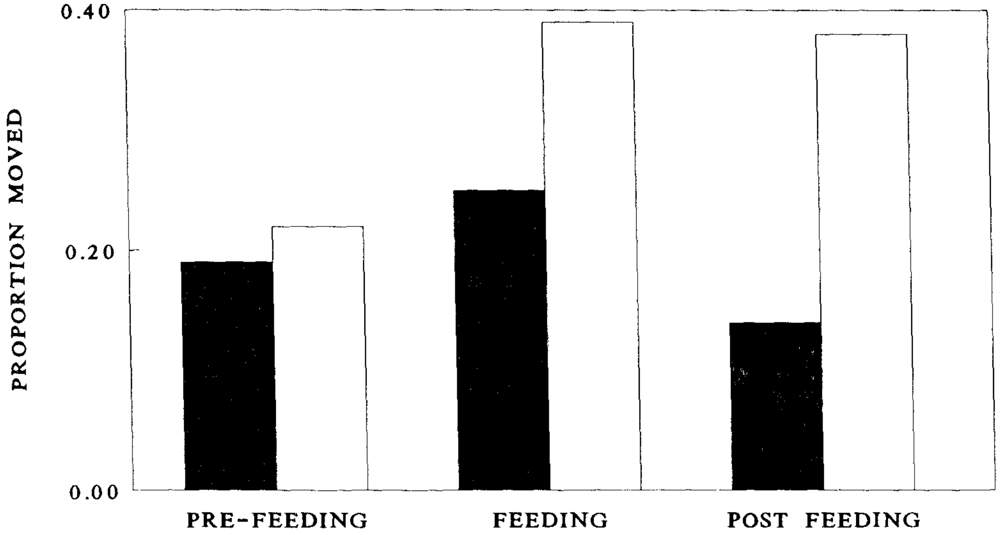

Figure 4.—Influence of the field food-supplementation experiment on *Argiope keyserlingi* movement. The data are partitioned into three periods: 1. the pre-feeding control period of four days, spiders were marked and observed but not manipulated; 2. the feeding period of four days where ½ of the individuals (all adult females) were provided with supplementary food; 3. the post-feeding period of five days where the manipulation ceased but the spiders were monitored. Data are the totals at the end of each period. The solid bars represent the spiders that were provided with supplemental food, the open bars represent control spiders. Each treatment group began with 40 spiders; sample sizes declined between periods because of spider mortality (Fig. 5).

ished, but this difference was not statistically significant (G-test, *ns*; Fig. 5). This difference was more apparent during the post-feeding period (Fig. 5) and it was statistically significant (G-test, $P < 0.001$).

Of the spiders surviving at the end of the season, 41% of the fed group produced at least one egg case whereas only 25% of the unfed group did so (Table 6). There was no significant difference between treatment groups in either the number of spiderlings per egg case or the total number of spiderlings per female (Table 6). Several of the females from each treatment group captured large prey items (in addition to the supplemental food). One of the no-supplementation females captured an unusually large prey item (large Asilid fly). This fly represents the largest single prey item recorded during this study (0.12 g), and this spider also had the highest reproductive output recorded from a female *A. keyserlingi* during this study (850 spiderlings from three egg cases). If this exceptional female is removed from the analysis, the reproductive output per female among the experimental females that were provided with supplementary food is greater than the reproductive output of those which were not fed (Table 6).

DISCUSSION

Three lines of evidence indicate that relative foraging success largely determines differences in survival and reproduction patterns among female *A. keyserlingi*. First, individual females kept in the laboratory showed a direct response to feeding treatment. The high food treatment females grew larger and were more fecund than those females maintained on the low food diet. Second, twice as many females provided with supplementary food in the field experiment succeeded in completing at least one egg case. In addition, if the single unfed female which happened to capture a very large prey item is discounted, there would have also been a significantly greater reproduction among fed females. In one sense, the exception proves the rule; this individual captured the largest prey item observed in the study and exhibited the record highest reproductive output. Foraging success is unpredictable but crucial to female *A. keyserlingi*. Another conclusion from the field experiment is that mere survival is not sufficient to insure successful production of eggs or juveniles. Only 25% of the surviving females that were exposed to natural prey abundance actually produced egg

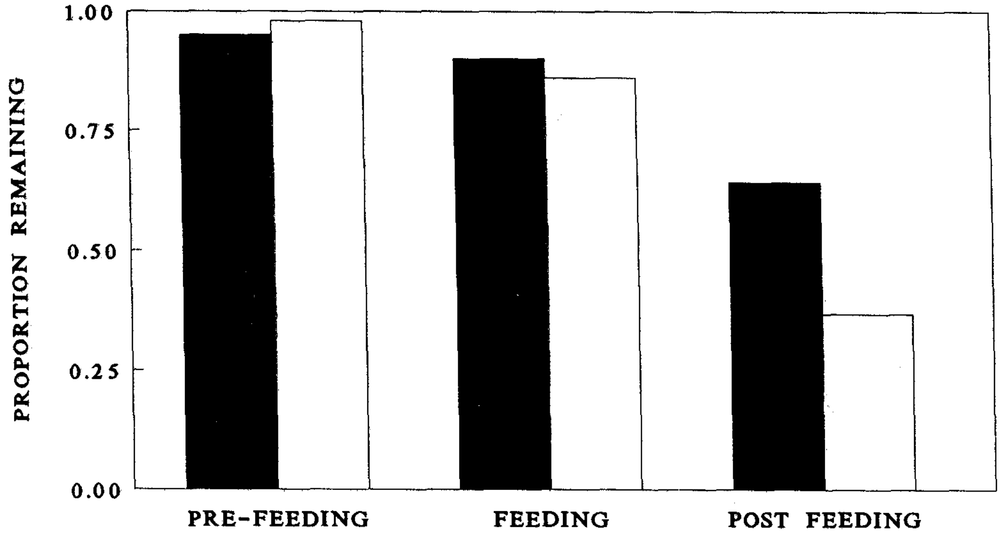

Figure 5.—Influence of the field food-supplementation experiment on *Argiope keyserlingi* survival. The data are partitioned into three periods: 1. the pre-feeding control period of four days, spiders were marked and observed but not manipulated; 2. the feeding period of 4 days where ½ of the individuals (all adult females) were provided with supplementary food; 3. the post-feeding period of five days where the manipulation ceased but the spiders were monitored. Data are the totals at the end of each period. The solid bars represent the spiders that were provided with supplemental food, the open bars represent control spiders. Each treatment group began with 40 spiders. Because of the intensive search effort by five observers and the relatively small area of suitable habitat, disappearance is probably a good measure of survivorship. Individuals classified as "absent" were assumed to be dead.

cases. Third, the mortality rate among *Argiope keyserlingi* was lower for individuals provided with supplementary prey in the field. Mortality was assessed by disappearance; it is possible that if some spiders moved and were not re-located they would have been misclassified as dead. Because there were four observers searching a limited patch of relatively sparse habitat, I believe that few individuals of this conspicuous spider were missed.

What could cause increased mortality? It is possible that individuals with poor foraging success starved to death, but this seems unlikely. Individuals maintained in the laboratory survived on low food for a period well beyond the scope of this experiment. When individual *Argiope* die from starvation, they are found hanging from their webs or in the vegetation below. Dead spiders were rarely found. It seems much more likely that they suffered increased risk of predation. Visually hunting predators, including diurnal birds and wasps (*e.g., Cryptocheilus* sp.), are more likely to notice moving spiders. Vollrath (1985) suggested that movement to a new

Table 6.—Fecundity of *Argiope keyserlingi* females from field manipulation experiment. Figures based on the number of females that remained and produced at least one egg case (number that laid any eggs). The number of juveniles was based on a total count of active juveniles that emerged (all cases combined). Unfed (subset) treatment group recalculated excluding the single female that captured the record largest natural prey item.

Treatment group	Original *n*	Number at end of experiment	Number that laid any eggs	Number of egg cases per fecund female ($\bar{x}$)	Number of spiderlings per case $\bar{x}$ (SEM)	Number of juveniles per female $\bar{x}$ (SEM)
Food added	40	22	9	1.2	293 (34)	147 (66)
Unfed	40	16	4	2.0	290 (43)	145 (137)
Unfed (subset)	39	15	3	0.6	294 (122)	98 (118)

web site increased the risk of predation for *Nephila clavipes* (Linnaeus), and that individuals provided with supplementary prey moved less and suffered a lower rate of mortality. As adult female *Argiope keyserlingi* become sated with food their behavior changed; they ceased rebuilding the sticky-orb each morning and they moved to a retreat in a curled leaf near the upper attachment point of the web. This shift probably made them far less obvious to a predator hunting for spiders in a web. Several of the adult females that were in the food supplementation treatment group quit foraging after only two days of extra food. These spiders remained in their retreat until they laid eggs. Increased foraging success would thus reduce the apparent exposure of a female to predators which search webs, and might account for the lower mortality in the fed group that was evident only towards the end of the experiment because the mortality effect would be cumulative (Fig. 5).

Do patterns of activity and habitat selection in *A. keyserlingi* reflect prey abundance or habitat, or both? There is some evidence from this study that the annual phenology of *Argiope keyserlingi* is related to seasonal variation in prey abundance. Spatial distribution of spider density was, however, not related to prey abundance patterns. If the data are analyzed treating each date and plot as a separate sample, there seems to be little relationship between *A. keyserlingi* and potential prey. *Argiope* are most active when prey are most abundant, but not necessarily in sites with highest prey numbers. There was no serial-autocorrelation in the sticky-board insect samples in this study, suggesting that prey were unpredictable in time and space. The inconsistency in prey numbers between years across plots apparently obscures any more general seasonal relationship between spider density and prey abundance. In a comparison of *Argiope aurantia* Lucas and *A. trifasciata* (Forskal), McReynolds & Polis (1987) concluded that differences in habitat and prey handling abilities explained the small dietary differences between these two species. Differences in diet reflected both seasonal change in the prey available as well as the size relationships between growing spiders and the prey that they were capable of handling (McReynolds & Polis 1987). Few of the measured web characteristics were correlated with the taxa of prey which were captured (McReynolds & Polis 1987). My results with *A. keyserlingi* appear consistent with those of McReynolds and Polis insofar as the fact that prey captured seem to reflect seasonal prey availability. I do not have any comparable information on individual prey capture rates, or the relationship between spider size and prey captured.

Although *A. keyserlingi* reproduction seems to be closely tied to the biomass of prey captured, there was no evidence indicating that *A. keyserlingi* exerted control over prey density. This situation resembles a donor-controlled system (Pimm 1982). Pimm (1982) suggested that this sort of relationship should be rare (with the exception of detritivores). The fact that *A. keyserlingi* abundance appeared to have had little effect on prey density might be because this orb-weaving spider was only one of many predators that influenced insect abundance in the study area. Alternatively, this may be related to the fact that the density of *Argiope keyserlingi* was low compared to estimates for other *Argiope* species which average 40 to 50 times higher than those measured in this study (Olive 1980; Brown 1981; Horton & Wise 1983). Thus there may be too few *Argiope keyserlingi* present to have exerted control over insect abundance.

Argiope keyserlingi density was related to general habitat features, especially those associated with web-site availability (*e.g.*, *Xanthorrhoea* density). The importance of *Xanthorrhoea* shrubs as web sites may be related to the fact their structure, with a brush of long (1 m) narrow (1–6 mm) leaf blades spreading radially from a central trunk, provides an infinite gradation of gap sizes which can accommodate webs of many sizes and orientations. There was no correlation between these preferred sites and potential insect prey abundance. If prey are not predictable and there is high mortality among adult females in their webs, it is possible that *Argiope* choose web-sites as much to avoid predation as to maximize prey capture rate. In light of this, it would be interesting to investigate the influence of web position on the risk of predation.

Overall, these data support the idea that vegetation structure is the chief determinant of web-site choice for orb-weavers, rather than prey availability (Enders 1973; Colebourn 1974). Three of four orb-weaver species studied by Pasquet (1984) exhibited a clear relationship between density and habitat structure, while only two species built webs where prey abundance was highest. Furthermore, vegetation structure but not prey availability was found to be a very important predictor of spider community structure (Greenstone 1984). In a study comparing the spider assemblages on three continents, Rypstra (1986) found that vegetation structure was the best predictor of spider activity. Prey abundance was also significantly correlated with spider activity at each locality (Rypstra 1986). Riechert & Gillespie (1986) reviewed the basis for web-site selection taken from the literature including data from 14 species of araneids. Vegetation was a web-site selection criterion for 12 of these 14, while prey abundance was important for only 5 of the 14 species. In the sheet-web building agelenid *Agelenopsis aperta* (Gertsch), web sites are the subject of intense intraspecific competition; and there was a clear positive correlation of favorable web sites with both physical and prey-capture criteria (Riechert 1974, 1976, 1977, 1979, 1981). It is clear that in cases where vegetation and potential prey covary, inference about their relative importance is difficult. Rypstra (1983) demonstrated that both web-substrate complexity and prey abundance are important to equilibrium spider density within enclosures. In this case, prey appear to be a more important determinant, but this result is partially explicable by reduced interspecific predation and cannibalism among the spiders in the enclosures maintained under the high food regimes.

My results reinforce the general conclusion that vegetation structure is an important predictor of orb-weaving spider abundance. Prey abundance appears to be of lesser significance in relation to spider density, but this may not indicate that it is less important to the spiders. As Rypstra (1986) points out, vegetation is easier to quantify; and I would add that it is probably less variable in space and time than insect abundance. Perhaps the difficulties involved in precise quantification of prey availability are an important confounding factor in broad-scale community analyses. Prey variability is real and it is possible that spiders are constrained to use a more reliable factor (vegetation) in their efforts to select profitable foraging sites. An indication that prey encounters influence *A. keyserlingi* behavior is that web-site movement was related to success in capturing prey. Individuals provided with supplementary prey were more sedentary (Fig. 4). Similar results have been observed in other orb-weaving spiders in the field (Olive 1982; Janetos 1982; Vollrath 1985). In contrast, there was no relationship between dietary experience and movement in laboratory experiments on *Nephila clavipes* (Vollrath & Houston 1986).

Gillespie & Caraco (1987) found that individuals of *Tetragnatha elongata* Walckenaer in a prey-rich environment actually moved more than those inhabiting a relatively depauperate area. Their results appear consistent with the predictions of a risk-sensitive foraging model where movement will increase as prey availability exceeds an appropriate physiological requirement. The behavior of *Tetragnatha elongata* apparently does not match a second model described in their paper, which predicts that spider mobility would be inversely related to prey availability. The key difference between these two models was whether a foraging spider used capture success information to predict the best strategy. According to these authors the first model assumes that temporal variation in prey abundance makes it difficult for a forager to predict spatial prey distribution. Hence if prey availability is high, spiders will benefit by sampling several localities. Results for *A. keyserlingi* appear to conflict with Gillespie and Caraco's result. Temporal variation in prey abundance appeared to mask spatial predictability, and prey abundance was limiting to female *Argiope*. Nevertheless, individual female *A. keyserlingi* moved more often when their foraging success was poor.

Interpretation of the present study depends upon the scale of observation. On a broad scale, there was a positive relationship between *Argiope keyserlingi* seasonal phenology to temporal prey-abundance patterns. On a finer scale, there was little relationship between prey abundance and the number of active foraging spiders on individual sampling plots. At this scale, spider density seems to be related to the availability of preferred sites for the construction of webs. At the scale of individuals, the history of foraging success predicted both survival and reproduction, and had a dramatic influence on behavior.

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