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Selection of Habitat by the Spider Argiope aurantia Lucas (Araneidae)

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ABSTRACT: Visual search for the webs and egg sacs of *Argiope aurantia* Lucas showed that it is most abundant in dense perennial vegetation. This pattern of distribution was confirmed by release of the species in selected plant communities: more spiders remained in densely vegetated sites than in sparsely vegetated ones, both in the 2nd instar and in middle immature instars; but adults and subadults left densely vegetated woodlands to build webs at the edge of those woods. It is suggested that wind reduction is the significant stimulus to immatures, and light, to adults.

INTRODUCTION

Argiope aurantia Lucas is among the commonest of spiders, locally known as the "writing spider" due to the presence of a vertical white mark in its orb web. This spider has been reported from a broad range of habitats, including grasslands and woodlands (Fitch, 1963), and from the edges of bodies of water to dry grassy hillsides (Levi, 1968).

The use by this spider in the daytime of a fixed web allows easy determination of its location. The vertical mark of silk in the web, the bright yellow and black markings and large size of the adult, the large web of the adult and the exposed position in which the egg sacs are placed — all contribute to make this spider easy to find by visual search. Beating with a net, used by earlier workers, actually collects only a small fraction of the spiders of this species observed to be in an area. In large part, this is due to the fact that the spider jumps out of its web, which is near the ground, when vegetation nearby is disturbed.

Here, I describe the population density of this species in the range of habitats occupied in North Carolina, as determined by visual search. By the release of this species in various plant communities, I tested the idea that *Argiope aurantia* is restricted to stands of plants having a particular physical structure.

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DISTRIBUTION OF ARGIOPE AURANTIA AMONG PLANT COMMUNITIES

Methods.—From 1968 to 1972 I spent several days a week in the Raleigh-Durham area of North Carolina searching for *Argiope aurantia* and other orb-weaving spiders. Searches were sometimes conducted by beating the vegetation with a net, but, more often, visual searches were made.

In February and May of 1971, I made systematic searches for the egg sacs of *Argiope aurantia* in the largest accessible stands of the early stages of old-field succession. I walked a minimum of 100 paces through an area of uniform vegetation from a point of access, usually a road. I walked toward any egg sac that I spotted and collected it. I recorded the sort of vegetation that dominated the area searched, the number of paces walked, and the number of egg sacs collected. This gave an index to the relative abundance of *Argiope aurantia*.

Results.—This spider was quite rare in old fields before trees and shrubs invaded (Fig. 1). After shrubs were present, the spider reached "moderate" densities, *i.e.*, levels of egg sac density at about the average (dotted line) for the middle group of plots in Figure 1. The levels of density of webs that prevailed in those plots earlier in the year are also considered moderate. The spider disappeared from the plant communities of succession by the time the tree canopy closed over. This spider reached "high" densities in road cuts covered with sericea lespedeza (*Lespedeza cuneata*). The density of webs counted on randomly selected plots in these lespedeza areas ranged from 11.7/sq m

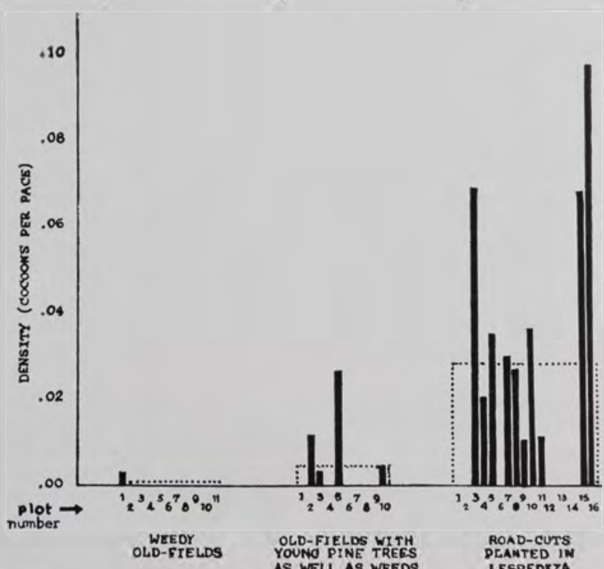

Fig. 1.—Density of the egg sacs of *Argiope aurantia* in different sorts of plant communities. The dotted lines represent the total number of egg sacs found in each sort of plant community, divided by the total number of paces taken to collect the egg sacs. One pace is approximately 0.75 m in length. The small bars above each number represent the density of egg sacs in particular stands

in May of 1971 to 1.6/sq m in September 1970 (Enders, 1972). The highest density of egg sacs reached in an area with no shrubs or trees present was part of an old dump; that high density may be the result of the disturbance of secondary succession.

My other observations show the same pattern of distribution of *Argiope aurantia* as the systematic search for egg sacs. I was regularly able to find low densities of immatures and adults of this species in fields abandoned the previous year, provided the dead plants had not been plowed under. But I never found this species in fields of annual crops: soybean, sorghum, maize and tobacco. I also found it at low densities in a cattail (*Typha*) marsh. Although I found no *A. aurantia* in woodlands until 1971, in July of that year I found six animals in a mixed hardwood-pine forest. This forest was adjacent to an extremely high density population of the spider in lespedeza, the second black bar from the right, in Figure 1. The density of the species in this woodland was about a thousandfold less than in the neighboring lespedeza area, which had been sampled by searching randomly selected plots. Although I left the spiders in the woodland, I could find neither spiders nor egg sacs there later in the year, despite repeated searches of both the area near the ground and the canopy of the forest.

In coastal North Carolina (Beaufort and Cape Hatteras areas), I found *A. aurantia* in moderate density in two places: (1) *Baccharis* with *Ammophila,* where a sand dune bordered a salt marsh; and (2) in a stand of *Myrica* and an unidentified grass, overgrown with *Smilax*. Both stands were shrubs mixed with grass, as the stands in old-fields which had moderate densities.

High densities of immatures were found in two places: (1) the edge of thickets (*Ilex* and *Myrica*) bordering a *Juncus roemerianus* marsh; and (2) *Myrica* thickets, 2 m in modal height, with herbs covering an (estimated) 15% of the stand. At the coast, I did not find *A. aurantia* in stands of climax forest or in any stands of grasses that lacked shrubs.

Everywhere I found *A. aurantia* quite regularly in areas disturbed by man: gardens typically supported low densities, especially where weeds were present. Weedy roadsides as far S as Hunter's Island, S.C., supported populations at all levels of density. Moderate to high densities were found wherever large stands of planted lespedeza were present at the edge of four-lane highways. These included road cuts S of Fayetteville, N of Winston-Salem and W of Asheville, N.C. This species was observed on road cuts as early as the second summer that vegetation was present.

A. aurantia was found in early stages of plant succession, even in 1st-year abandoned fields, but its highest densities were reached where shrubs had already invaded the plant community. In woodlands it occurred only as immatures at very low density, adjacent to an extremely high density population in lespedeza. The extreme high densities recorded in less disturbed areas of vegetation approximated the usual high densities in stands of lespedeza on road cuts.

RELEASES

Methods.—I collected egg sacs of *A. aurantia* in the winter of 1970-71, and stored them in refrigerators. In May, after this species had emerged out of doors, I placed the stored egg sacs at room temperature. When these spiders emerged, I spread them over the vegetation near the ground in adjacent stands of plants at Clayton, N.C. These included a soybean field (rows, 1 yard apart; average height of plants, 14 cm), a heavily shaded swampy hardwood-pine forest with dense undergrowth, the weedy edge of the woodland with the soybean, and a road covered with dense crabgrass (*Digitaria* sp.) about 15 cm tall. Additionally, at Raleigh, N.C., fewer individuals were released in a hardwood-pine forest, the edge of those woods, the bare ground of a parklike stand of pines (*Pinus taeda*), a maize field and a ryegrass field.

In June 1971, more spiders were collected from the lespedeza areas and marked with model airplane paint. They were released in the following sites at Raleigh: the hardwoods-pine forest, its edge and a pine plantation with closed canopy, no understory and considerable litter. These spiders were held in individual jars for about 28 hr after capture and marking. The jars were then opened at the release point in late afternoon and left on the ground. Any animal which did not leave its jar by the next morning was excluded from further consideration. Different color markings were used on spiders where releases were made repeatedly or in adjacent areas.

In August of 1970 and 1971, large females were released at the same hardwood-pine woodland and edge areas as in the June experiments at Raleigh. A pine woods used had a very dense understory of vines and was not the one used in June. These spiders seemed to be within 1 instar of sexual maturity, judging from the form of the clavus and the darkening of the front legs.

The day after all releases, the nearby area was searched for webs. The number of marked spiders which remained to build webs was recorded. However, any distinctively marked animal which turned up after the first search was added to that number. Similarly, the maximum number of webs of the unmarked 2nd instars used was recorded, even if it occurred a few days after the release. The 2nd instars had been released into areas where no naturally occurring *A. aurantia* were found. Naturally occurring animals could be distinguished because they were about an instar further along in their development than the releases.

Results.—The 2nd instars that were found remained within 2 m of the point of release; the immatures of the 2nd release, within 4 m; and the "adults," generally within 7 m. Only the adults could be found outside the plant community in which they had been released, in which case they had traveled more than 30 m to leave the woodlands.

Fewer spiders of the 2nd instar remained in the sparse vegetation of the soybean field, and fewer of the later instars remained in woodlands (Table 1). These two results are in sharp contrast to the consistently high percentage which remained at the woodland edge. In addition to the results presented in the table, 2nd instar spiders remained in the ryegrass field (planted the previous autumn), but not in this year's maize, or in the parklike stand of pines.

That the 2nd instar remains wherever dense vegetation is present was confirmed by the fact that release of 6000 2nd instars in the same soybean field in July resulted in at least 400 present on orb webs (estimated by counting webs in a sample of the field). At this time, the soybean had reached a height of about 30 cm, with considerable density of vegetation.

The late instars do not remain in deciduous woodlands: except for one which built in the canopy of the forest, all left the mixed hardwood-pine forest on the night of release or the next night. Nine of this group were found that had moved from woodland release point to the edge of the woods, a minimum of 30 m. Of these, four were not found until the 2nd day after release. One animal climbed to the top of the hardwood-pine forest and remained 8 m above the ground for about a week. This species had never been reported to build its web at so great an elevation. The fact that some adults remained in the pine woodland may be related to the fact that some large trees had fallen there — the webs of the spiders which remained there were not in heavy shade, as were the webs built in the hardwood-pine woodland.

In cases where spiders left release points, no predation on the spiders was ever observed. Also, once the spiders built webs, predation would result in an empty web: an unusual rate of appearance of empty webs (or unusual rate of mortality of spiders) was not observed in the groups of spiders which remained at release points. Instead, upon release spiders could be regularly observed walking (on vegetation, ground or silk) or "ballooning" (Kaston, 1948) away from the release sites. When the tall grass was mowed where the "edge" releases of August 1970 had built webs, many spiders moved the 20 m to unmowed areas. Otherwise, animals which once built webs, including 2nd instar spiders, were found regularly at or near the same sites for several weeks after release. During the releases reported above, no

TABLE 1.—Per cent of *Argiope aurantia* spiders which remained in various plant communities after being released there

Plant community Month	Instar	Hardwood-pine forest	Pine forest	Edge of hardwood-pine forest	Dense crabgrass	Soybean field
May	2nd	14% (3/22)		12% (5/42)	14% (5/36)	0.5% (2/384)
June	4th-7th	10% (2/20)	30% (7/23)	37% (7/19)		
August	8th-11th	9% (5/54)*	24% (4/17)	74% (17/23)		

* All five which remained in woodland left the 2nd night after release

immatures were found at any distance from the point of release. However, on one occasion several marked 6th instar immatures were found again about 10 m away from their point of release. This was after an abortive attempt to demonstrate aggregation in which an area of an old field had vegetation removed except for one stem every 0.5 m, an area 5 m x 5 m. These observations support the idea that the disappearance of released spiders was due not to unusually high predation, but to their dispersal from areas which they "judged" to be unsuitable.

Discussion

Other authors have reported *Argiope aurantia* from the savannah and early seral habitats in which I found this species (Kaston, 1948; Lowrie, 1948; Muma and Muma, 1949; Barnes, 1953; Barnes and Barnes, 1955; Fitch, 1963; Berry, 1967; Levi, 1968). When earlier workers attempted to take spiders in a regular manner from the different stages of plant succession, not many specimens of this species were taken (Lowrie, 1948; Berry, 1967). Nor have summaries of museum collection data by Kaston (1948) and Levi (1968) provided a clear, consistent statement of the occurrence and relative abundance of *A. aurantia* in different sorts of fields.

Fitch (1963) stated that *A. aurantia* "is more tolerant of shade than *A. trifasciata,* but less tolerant of exposed situations with sparse vegetation." My own observations of *A. trifasciata* (Forskal) indicate that this species does occur at slightly earlier stages of succession, on the average, than *A. aurantia.* Both my observations of habitats occupied by *A. aurantia* and my releases of that species support Fitch's statements. Therefore, Fitch (1963) and I disagree with Kaston (1948), who did not note any difference between these two species in the range of habitats occupied, and with Levi (1968), who suspected that *A. trifasciata* occurred in drier habitats. The data gathered by Lowrie (1958) and Berry (1967) are insufficient to determine the relative habitat distribution of these two species; in fact, beating with a net is an inadequate method for these two species, since one captures relatively fewer *A. aurantia* than *A. trifasciata,* in areas where the densities of each have been estimated by the visual search of randomly selected plots. Release of marked *A. trifasciata* in selected habitats can neatly demonstrate any difference between the two species in the type of habitat that is acceptable.

My releases of *A. aurantia* demonstrate that this species actively selects certain habitats, characterized by dense vegetation near the ground that is not heavily shaded in late summer. No pattern of choice of particular species of plants was found. The range of habitats thus chosen corresponds to that described by Fitch (1963) and found by my visual search for the species.

The maximum recovery rates of released spiders reported here, 14%, 37% and 74% at different instars, may be related to the (differing) abilities of spiders (of different sizes) to disperse by "flying" on silk (ballooning, Kaston, 1948). Adult *A. aurantia* cannot balloon; I have seen middle instars balloon horizontally; 2nd instars can balloon vertically by using very slight thermal air currents. If a spider balloons only a few meters, it becomes virtually unfindable for me. Moreover, spiders which balloon vertically can travel hundreds of kilometers, since ballooning spiders have been collected several kilometers above the earth's surface (Glick, 1939). Moreover, the fact that this species normally disperses from the location of the egg sacs in the springtime can explain the very low fraction of 2nd instars which remained even at the most densely vegetated sites of release. Due to the natural occurrence of large numbers of egg sacs of *A. aurantia* in areas of lespedeza, I could not conduct releases in such areas, and I could not make observations there of dispersal from single egg sacs. However, observations of the densities of webs of 2nd instars under egg sacs in lespedeza suggested that dispersal under natural conditions approximated that observed during the releases. There was no marked clumping of the webs under the egg sacs, while high densities of webs, like that within 2 m of release points, prevailed throughout the lespedeza.

Only the larger-sized spiders left woodlands, though in laboratory gradients all stages are positively phototactic (Enders, 1972). It may be that in later life a positive response to light is no longer held in check by a negative response to wind. Enders (1972) has presented some evidence that the apparent response to vegetation density is via the presence or absence of wind. Fortunately, the spider's negative response to wind was at least partially separable from the other, confounded, microclimatic factors (temperature and humidity), since the araneid spiders tested prefer dry places, in gradients of humidity (Enders, 1972; *see also* Cherrett, 1964).

The results described in this paper support the idea of Duffey (1966) that spider species select the structure of the habitat as well as the microclimate of the habitat. The stimuli which seem to determine whether a habitat is acceptable to *A. aurantia* would ordinarily be controlled by the structural characteristics of the habitat: vegetation density nearby, as well as at the actual web site, controls wind, while light is controlled by the arrangement of the vegetation density into strata which may shadow the ground. *A. aurantia* and most other araneid spiders are very tolerant of desiccation and ordinary temperature extremes (Duffey, 1962). I, therefore, suggest that structural characteristics of the environment are the primary influences upon web site selection by members of the family Araneidae, while microclimate is of minor importance. In contrast, Riechert (1973) suggests that thermal budget is of prime importance for a desert spider of the family Agelenidae. However, (1) the species of agelenid may be a special case, since temperature must be of importance to any animal in a hot desert, and (2) agelenids and araneids are adapted to microhabitats having much different exposure to desiccation. Agelenids' webs occur near the ground or inside herbage, while araneids build aerial webs in spaces exposed to the elements (Duffey, 1962). In fact, an agelenid species I tested showed a preference for the moist end of humidity gradients, while araneids preferred the drier end (Enders, 1972).

Only in "edge" habitats did *A. aurantia* reach high densities of population: lespedeza, young bayberry (*Myrica*) and mixed salt marsh-coastal scrub. All these areas had a vegetation density that would induce settling by released 2nd instars, and yet none were shaded enough to cause adults to leave. Thus, each area had several years for colonization by ballooning *A. aurantia* and for the local population to build up, since about 13% of the 2nd instars remain near the place of emergence, in vegetation that is suitably dense (Table 1). In this manner, this species is favored by ecotonal situations, even though it can survive in the early stages of plant succession if no ecotone is present. For more than a century, the edges of roads have provided a suitable man-made ecotonal habitat (Wilder, 1873; Bilsing, 1920), while before that the edges of bodies of water must have been the prime ecotone available. Though the excellent dispersal abilities of *A. aurantia* (Glick, 1939) must allow it to reach areas hundreds of kilometers away from the source, today's road system provides this spider a ubiquitous source for any large area of suitable perennial vegetation that develops during plant succession. As there are a considerable number of species of spiders that utilize similar successional and ecotonal habitats (Berry, 1967), there are implications for the management of habitat diversity to reduce insect numbers (de Loach, 1970). Hedgerows and early planting of crops should favor *A. aurantia,* while monoculture and the manicuring of road edges should reduce its numbers considerably.

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