

Enders, F. 1976. Effects of prey capture, web destruction and habitat physiognomy on web-site tenacity of *Argiope* spiders (Araneidae). J. Arachnol. 3:75-82.

EFFECTS OF PREY CAPTURE, WEB DESTRUCTION AND HABITAT PHYSIOGNOMY ON WEB-SITE TENACITY OF *ARGIOPE* SPIDERS (ARANEIDAE)

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ABSTRACT

Both in the laboratory and in the field prey capture did *not* have a strong influence upon web-site tenacity of *Argiope aurantia*. But experimental web destruction increased the probability that *A. aurantia* changed its web-site, perhaps only due to the physical displacement of the spider. Removal of vegetation near the web of immature *A. aurantia* resulted in most of these spiders leaving their web-sites, especially in areas less sheltered from the wind. *Argiope trifasciata*, in contrast, did not leave web-sites after removal of nearby vegetation.

INTRODUCTION

Spiders often remain at the same web-site from one day to the next (McCook, 1889; Enders, 1975). Yet, little is known which factors might influence the probability that a spider will stay at a particular site. "Web-site tenacity" is defined as the per day probability that a spider remains at the same web-site, or the number of changes of web-site divided by the number of observations of webs from one day to the next (Enders, 1975). The total number of changes of web-site includes animals found again nearby and also those which both take up their web and disappear from view. Thus animals which apparently have died are excluded from the calculation, since mortality of *Argiope* spiders is normally marked by the disappearance of the spider coupled with the persistence of the old web.

The initial and subsequent choices among habitats by the web spider *Argiope aurantia* (Araneidae) have been described (Enders, 1973). And some speculation is available regarding the use of prey and habitat as resources by various araneid orb web spiders (Enders, 1974, 1975b). Turnbull (1964) reported a strong effect of prey abundance on web-site tenacity of *Achaearanea tepidariorum* (Theridiidae). But other studies (Araneidae: Cherrett, 1964; Colebourne, 1974; spiders in general: Duffey, 1966) have emphasized the greater importance of habitat structure (physiognomy or architecture) for selection of web-sites by spiders. Field observations of *Argiope aurantia* (Enders, 1975a) revealed no marked influence of prey capture on web-site tenacity. Here, I report my experimental studies which estimate the relative importance of prey capture, web destruction and habitat physiognomy on web-site tenacity of *Argiope aurantia*. I include a few

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observations on *A. trifasciata* for comparison with a species which selects less densely vegetated habitats than *A. aurantia*.

FIELD EXPERIMENTS ON THE EFFECT OF FEEDING

Methods—The study areas used were the edges of road cuts, where large numbers of *Argiope aurantia* occurred, near Raleigh, North Carolina. Areas were dominated by the herbaceous perennial plant *Lespedeza cuneata* and are described in greater detail elsewhere (Enders, 1972; 1974).

Different feeding rates were maintained for three groups of spiders in the field: (a) “no prey,” by removing any prey noticed in the web; (b) natural feeding rate, or whatever entered the web by itself; and (c) prey always present in the web, by adding to what the spider captured, roughly tripling the intake of prey biomass from group b. Spiders were originally assigned to treatments alternately. As the original spiders disappeared from particular treatment groups, the nearest available unmarked spiders were used as replacements.

Treatments were applied twice a day, late morning and late afternoon (evening). Insects added to the web were usually grasshoppers slightly longer than the spiders, or else several houseflies. Since most natural prey (the most abundant, bees, grasshoppers and chauliognathid beetles) were kept in the web at least half a day, and since virtually no prey was taken during the night by *Argiope* spiders, the treatment schedule should have been effective to influence spider feeding rates. Two replicates of this experiment were performed, one during the period 22 to 25 June 1970 (using middle stage immatures) and the other 6 to 11 September 1970 (adult spiders). One additional experiment was done feeding spiders water sweetened with table sugar (Bays, 1962), but the negative results of that feeding replicate might be due to insufficient caloric uptake by spiders, even though the sugar water was accepted by them.

Results—Different levels of feeding could not be maintained every day because spiders occasionally refused to attack any insects offered. This occurred primarily in the June replicate. Analysis of results using only the actual feeding status of the spider did not change the conclusions. Only one statistically significant effect was found in eight statistical comparisons made (by chi square test, Snedecor and Cochran, 1967). The extreme comparison between prey removed and prey added groups for the September experiment indicated a 7% increase of web-site tenacity (Table 1), with p between 0.05 and 0.025.

LABORATORY EXPERIMENT ON THE EFFECT OF FEEDING

Methods—A cage was made 2.3 m high, 2.3 m wide and 4.6 m long from translucent plastic sheets stapled onto an exterior 5 cm \times 5 cm wood frame. This cage was sealed by plastic tape along the seams, and the only entrance was a zipper sewn into one edge of the cage. The zipper was opened only once a day, in order to give the spiders water from a syringe and to feed them. The room containing the cage had a photophase of 16 hours, and an air conditioner running for three hours during the morning to provide a regular cycle of temperature.

Four marked (with fast-drying paint) *A. aurantia* taken from the field were released on successive days in different corners of the cage, starting on 1 July 1970. The spiders climbed to the top of the cage along the tape and built webs in the upper corners of the cage. Two spiders could and sometimes did build webs in the same corner.

Table 1.—Summary of feeding experiments with *Argiope aurantia* in the field. Web site tenacity is the percentage probability a spider remains at the same web-site from one day to the next.

Treatment Group	Web-site tenacity	
	From initial day to the second day of observation (% of individuals)	% of all observations of which animals remained at same site
Prey removed	90 (n=1)	90 (n=90)
Whatever spider caught by self (control)	96 (n=28)	87 (n=87)
Prey added	95 (n=20)	93 (n=93)

The cage was centered below the lighting fixture which had 320 watts of fluorescent lighting. The entrance of the cage was away from the single boarded-up window, but near the door of the room. Only those spiders which built webs in the front right or back left corners were fed, a housefly a day. This arrangement neutralizes the effect of any gradients of light, noise, etc., which might have influenced preference for the corners in consequence of the location of door, light, window, and window air conditioner.

Results—Not even a small increase of web-site tenacity with prey catching was observed. Additional spiders in individual cages and a second four-spider replicate in the large cage which lasted only 20 days also revealed no difference in web-site tenacity of *A. aurantia* in fed and in unfed corners. Instead, spiders moved out of corners in which they had been getting flies, as well as moving into them. In the course of the completed four-spider experiment, one spider was eaten by another, two emaciated spiders starved to death, and one well-fed spider died after several months on its web. In addition those spiders, including two *A. trifasciata*, that were starved but watered regularly did not show any decrease in web-site tenacity with time. Starvation did result in a reduction of frequency of renewal of webs as animals were near death.

EFFECT OF WEB DESTRUCTION AND OF DISTURBANCE IN *ARGIOPE AURANTIA*

Methods—This experiment was performed at the edges of lespedeza-covered road cuts. The treatment was total destruction of the web each day, while the spider was left wherever it went. The spider's dragline which had been attached to the web was destroyed, so that no silk spanned the original web-site, but the spider was left on the vegetation whenever possible (most instances). The disturbance treatment is that certain nearby spiders were placed into individual jars, carried to the laboratory, taken from the jars, weighed, transported back to the web-site, and released in their original webs. Treatments were applied just after dark, and the spiders of the disturbance group were returned to their webs after 2-3 hours. Every third spider found was placed in the same treatment group (web destroyed, disturbance and control). Each spider was marked with an individual pattern of rapidly drying paint, and was retained in its treatment group if it could be found the following day, at the old web-site or at a new one (web sites were marked with masking tape). Due to the disappearance of the original members of the groups, more spiders were added to each group on subsequent days. All spiders used in this experiment were females, mostly fully adult, from 21 September to 7 October 1969. Chi square not corrected for continuity (Snedecor and Cochran, 1967) was used to test

for statistical significance of treatment effects.

Results—No significant effect of the handling disturbance was found (Table 2). Those animals whose webs were destroyed left web-sites significantly more often than the controls, both the night following destruction of the web, and also on subsequent nights when webs happened not to be destroyed.

Table 2.—Web-site tenacity of *Argiope aurantia* in the field after web destruction and after handling disturbance (** = difference with control group statistically significant at 0.01 level; * = difference with control group statistically significant at 0.05 level).

Treatment group	Web-site tenacity	
	From initial day to the second day of observation (% of individuals)	% of all observations of which animals remained at same site
Web destroyed	33 (24)**	50 (54)**
Undisturbed (control)	91 (11)	71 (52)
Animal handled, web <i>not</i> destroyed	82 (17)	78 (45)
Dates on which web-destroyed animals were not disturbed	40 (10)*	54 (13)
Dates on which handled animals were not disturbed	88 (8)	88 (8)

EFFECT OF VEGETATION DENSITY ON *ARGIOPE* SPIDERS

Methods—Enders (1973) hypothesized that it was the density of the nearby vegetation and plant density in the plant community as a whole (habitat physiognomy) which controlled the occurrence of *A. aurantia* immatures, but not the occurrence of *A. trifasciata*. To test this, in July 1971 all vegetation was cut away in a band from 20 cm to 100 cm around the webs of spiders in the field. Bushes and branches of large trees to a distance of 4 m were also removed. Vegetation to which silk was attached was not removed, and, as in other experiments, I made a particular attempt not to disturb or damage the web or its inhabitant. As in other experiments, animals were used as they were found, with no exclusions. After initial experiments indicated color-marking to be superfluous, spiders were left unmarked. The location of the web was marked with masking tape, and the experimental site was also quite noticeable, in consequence of vegetation removal.

Results were planned to be compared with the known web-site tenacity of 80+ per cent (Enders, 1975a). In addition, three *Argiope aurantia* were left undisturbed at one study site to check that high web-site tenacity of undisturbed animals. The spiders used in this experiment were middle stage immatures, mostly being the sixth and seventh instars.

Two main study sites were used, one an old-field planted with pine trees and the other the center of a lespedeza-covered road cut. Within the old-field site two subsites were used, one a location with sparse vegetation with the nearest trees 5 m away; the second subsite had pine trees within 5 m of one another, that is, roughly four times the density of vegetation.

The old-field subsite with less vegetation probably had the greatest exposure to wind. The old-field subsite with more trees was expected to have less wind, and the road

cut could be assumed to be the most sheltered at the height where immature *A. aurantia* build webs (Enders, 1974). The latter study area was entirely protected from wind on one side by the upward slope of a hill; and this site was also sheltered even on the downhill side by vegetation which was considerably denser than the old-field vegetation present at the other experimental site. Some trees were present at about 10 m further uphill.

Results—Removal of vegetation greatly reduced web-site tenacity of the immature *A. aurantia*. This reduction of web-site tenacity was statistically significant, whether one used as control the three animals observed the same year (none of which changed web-site), or the 83% web-site tenacity for *Argiope aurantia* in the lespedeza area in July of the previous year (Enders, unpublished data). Casual observation of untreated animals nearby and of post-treatment spiders also indicated a high web-site tenacity of animals living in the old-field site.

The effect of physiognomy of the study site was also statistically significant and of large magnitude: none of 13 experimental animals in the weedy old-field remained on the following day, 44% of nine remained in the old-field with denser trees, and 63% of 19 in the lespedeza-covered road cut. Since the old web of spiders which disappeared could not be found and since several spiders which left experimental web sites were found nearby after the experimental treatment, those spiders which did not remain had apparently left the web-sites for other locations.

Finally, there was also a statistically significant difference between the species *A. aurantia* and *A. trifasciata*: records show that seven immature *A. trifasciata* had vegetation removed from around their web-sites at lespedeza (three animals) and old-field (four animals) areas, and no spider changed web-site or disappeared.

DISCUSSION

Different ecologically definable groups of spiders have various manners of hunting, but most spiders are sit-and-wait predators (Enders, 1975b). Exceptions are known primarily in errant, non-web spiders (chiefly clubionids and salticids; also smaller lycosids). Though web spiders are restricted to the web, even such species may effectively search for prey if they change web-site until they encounter a web-site with sufficiently high prey capture rate (Turnbull, 1964). My results detailed above suggest that prey capture has no such effect in the orb-weaving spider *Argiope aurantia*: field experiments do indicate the possibility of small 7% (but compounded daily) increase in web-site tenacity of mature *A. aurantia*, as a consequence of a range in prey capture rate equal to three times normal feeding rates, compared to virtually zero in the comparison group. This effect, while statistically significant (0.05 level) may be a purely random statistical effect (p actually only 0.4, considering eight separate statistical contrasts made by me using 0.05 level of probability as criterion), or the result of partial destruction of webs (see below) during removal of prey items from webs of the comparison group. I emphasize that field observations (three summers) and laboratory experiments (detailed above) give no support to the idea that web-site tenacity might be related to prey capture rate in *Argiope aurantia* (Araneidae). In other species of orb web spiders, Cherrett (1964) and Eberhard (1971) found, respectively, no relation of prey capture to web site use (several araneid species), and a negative effect of prey capture of web-site tenacity (one uloborid species; uses orb web made of different type of sticky silk). Therefore, it appears that these orb web spiders are not normally limited by prey abundance, so that they have not evolved a

positive behavioral response to capture of prey. In contrast, *Achaearanea tepidariorum* (Theridiidae, three-dimensional web) appears to live in areas where prey are sometimes locally limiting, since most houses (natural habitat for this species) apparently have a high variance and low mean of insect abundance (potential spider prey). Houses probably also offer a lower density of potential predators on the spiders, when the spider is off the web and moving from one web-site to the next. The level of selectivity for web-site, I argue, is determined by a balance between increased predation rate on web spiders off the web and the increased prey intake possible at a better web-site (see Morton, 1971; Safriel, 1972). Increased predation on web spiders when they are off the web is logically deduced from the many anti-predator advantages afforded by the use of a web, such as early warning of attack, familiarity with terrain, and the greater number of escape maneuvers compared to non-web spiders (shaking the web, running on the web, and jumping off the web). Robinson and Robinson (1973) have indicated they consider the use of a web by molting spiders to be related to the anti-predator advantages of a web. Thus, the increased rate of change of web-site in unfed immature *Achaearanea tepidariorum* (Turnbull, 1964) may be a special case among web spiders. Data on this species' unusually high metabolic rate (Anderson, 1970) and large clutch size (relative to the female's length, and relative both to other Theridiidae and to most spiders; Enders, 1976b), seem to support this interpretation.

Removal of nearby vegetation here resulted in a greatly reduced web-site tenacity of immature *Argiope aurantia*, but not of *A. trifasciata*. This response is part of the behavior, apparently in response to wind (Enders, 1972) which brings the former species to the immature's species-typical web-site near the ground (Enders, 1974) in dense vegetation (Enders, 1973). Wind reduction near ground level is discussed by Gloyne (1964). Witt and Reed (1968) and Anderson (1974) find web spiders able to conserve web size for several weeks and to live several months, without food. Therefore, it appears that habitat structure rather than food is the proximate factor involved in selection of web-site by most web spiders. Turnbull (1964) did not investigate the influence of physical structure (physiognomy) of the habitat. My results support the idea that habitat physiognomy may be as important to predatory arthropods (Duffey, 1966; Elton, 1966; Colebourne, 1974) as it is to (predatory) vertebrates (Klopfer, 1965; Wecker, 1963; Sale, 1969). Wind may be an important proximate factor for vertebrates also, as in the selection of patches of habitat by grassland birds (Cody, 1964, pp. 25, 70).

After experimental destruction of the webs of *Argiope aurantia*, the spiders moved to some place on the vegetation and remained still thereafter for a long time, often till dusk. "Natural" apparent destruction of webs of this species in the field was observed very rarely. My observations to date indicate that web-site selection by araneid spiders is a fairly undirected process, and may be unguided by previous experience with a site. Specifically, *Argiope* spiders removed by me from their webs (or placed in a different web from which the occupant had been removed) to only a meter away were never found to return to the original web and web-site. Burrowing spiders (mygalomorphs and lycosids) seem to have some knowledge of their surroundings (Kuenzler, 1958), and araneid spiders are able to find their way about on the web itself (Le Guelte, 1969) to their retreat. But since araneid spiders cannot be said to have any home range beyond the confines of the web, the simplest interpretation of the effect of web destruction upon web-site tenacity of *A. aurantia* is that the spider simply did not happen upon the same web-site when it began to put down the frame of the new web. Curiously, one web spider, *Agelenopsis aperta* (Agelenidae; Riechert, Reeder and Allen, 1973) can be flushed

some distance from its web. But that family of spiders is also intermediate to the non-web spiders both in clutch size and Dyar's constant (growth increment at the molt; Enders, 1976a).

It is interesting that *Argiope aurantia* shows a reduction of web-site tenacity after web destruction, for the period of a few days after treatment has stopped (Table 2). Perhaps the spiders are unable to locate a suitable web-site the first night, but that is doubtful. The time scale of a reduction of web-site tenacity seen after molting is also several days (Enders, 1975a). An errant spider, *Lycosa nordenskiöldi* (Lycosidae) also shows increased locomotion, but for only a few hours, and after being merely picked up (Enders, unpublished data). Thus, it appears that spiders show increased locomotion as a response to appropriately serious disturbances, such as web destruction (but not handling) in the case of a web spider, and handling, in the case of a lycosid species; and this response is on the order of days, for web spiders which can change web-site once a day, or hours, for errant spiders, which can walk at any time during their period of activity.

ACKNOWLEDGMENTS

This research was in part supported by NSF Grant GB-6246 to P. N. Witt, and is part of a thesis carried out under his guidance for the Ph.D. degree in Zoology at North Carolina State University. During preparation of the manuscript, the author was supported by NSF Grant GB-27152 to W. F. Blair. H. W. Levi, B. S. Gerschman de Pikelin and R. D. Schiapelli identified species mentioned here. S. E. Riechert and J. S. Rovner made helpful comments on the papers.

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