1992. The Journal of Arachnology 20:173–178

WEB ORIENTATION, THERMOREGULATION, AND PREY CAPTURE EFFICIENCY IN A TROPICAL FOREST SPIDER

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ABSTRACT. No correlation was found between the web angle and the directional web orientation (in relation to the sun) for the orb webs of *Leucauge regnyi* in the Luquillo Forest of Puerto Rico. These data suggest that the web angle of *L. regnyi* is not a thermoregulatory response. In addition, prey capture efficiency of sticky traps placed at the mean angle of webs of *L. regnyi* is compared with traps placed at vertical and horizontal orientations in three sites in this tropical forest. Prey captured in sticky traps indicate a trend of prey availability in this ecosystem: vertically oriented traps catch fewer prey than horizontal traps or traps at the mean angle of web orientations; at sites of little or intermediate ecological disturbance, mean angle orientations catch more prey than horizontal orientations. Although confirmation that traps and spiders capture the same types of prey is lacking, it may be that in this tropical forest system, more prey are made available to spiders with horizontal and nearly horizontal web orientations than to spiders with vertical webs.

INTRODUCTION

A number of orb-weaving spiders, including *Metabus*, *Tetragnatha*, *Conoculus*, *Uloborus*, *Gasteracantha* and *Leucauge*, weave webs that vary in their orientation relative to the degree to which they are in vertical versus horizontal planes (Eberhard 1971, 1989, 1990; Buskirk 1975; Chacon & Eberhard 1980). However, no conclusive explanation has been offered for this horizontal rather than vertical orientation (Eberhard 1990). It has been postulated that: 1) horizontal orbs receive less damage by the wind (Eberhard 1971), but others (Biere & Uetz 1981) found that wind did not affect web orientation; 2) the oscillations of nearly horizontal orb webs effectively intercept slow flying dipterans (Craig et al. 1985; Eberhard 1990); and 3) a more horizontal orientation may allow a spider to build closer to a microhabitat containing abundant prey (Eberhard 1990), or to utilize limited support structures for web building (Buskirk 1975). A correlation between web size and angle found by Eberhard (1988) may also be due to habitat structure. Some webs of varying angle, however, have been observed where structure is available for vertical webs and a non-vertical orientation does not appear to increase proximity to an advantageous microhabitat (Eberhard 1971, 1990).

Web angle may also affect rates of prey capture. Chacon & Eberhard (1980) and Craig (1987) discuss three factors determining the prey capture efficiency of a spider web: the probability of insect encountering the web, the absorption by the web of the prey's kinetic energy, and the retention of prey on the web. Vertical webs appear to be favored in at least the first and last of these criteria. Chacon & Eberhard (1980) found that vertical sticky traps in an open field caught nearly three times as many prey as horizontal sticky traps and twice as many as inclined (45°) traps. Eberhard (1986) suggests that horizontal webs decrease effective distance between silk strands for prey moving horizontally, and thus make such orientations energetically costly. Horizontal webs do not retain prey as well as vertical webs, since prey freeing themselves from strands of vertical webs tend to fall into lower strands (Eberhard 1989).

Habitat structure may affect this apparent relationship between web angle and prey capture. Spiders that build nearly horizontal webs occur in forest and edge microhabitats (Milne & Milne 1980), as well as across streams (Buskirk 1975) and in deserts (Eberhard 1971). Perhaps insect flight patterns differ according to habitat structure. Eberhard (1990) has suggested that horizontal webs may capture prey falling from above. Numbers of prey falling from above may be higher in a forest than in an open field, since forest vegetation grows to a height from which prey may fall and be intercepted by a web.

To date, most studies on the directional orientation (North-South) of orb webs have not emphasized prey capture efficiency, [but see Tolbert's work on *Argiope* (1979) and various studies of colonial *Metepeira* spp. (Uetz & Cangialosi 1986; Uetz 1989; Uetz & Hodge 1990)]. Most studies attribute a thermoregulatory role to the directional orientation of webs (Carrel 1978; Tolbert 1979; Biere & Uetz 1981; Caine & Heiber 1987). Yet only a few studies have speculated on possible thermoregulatory aspects of web angle (vertical vs horizontal): Krakauer (1972) suggests that the slight angle of the webs of *Nephila clavipes* facilitates postural thermoregulation, and Tolbert (1979) argues that a vertical orientation allows a spider to heat up rapidly early and late in the day by exposing a large surface area to the sun, and keeps it from overheating at midday by exposing a small surface area to the sun. Thus there may be important thermoregulatory aspects of web angle. Specifically, the interaction of vertical angle and directional orientation may affect the surface area of the spider exposed to direct sunlight, and may, therefore, play a thermoregulatory role.

The tropical orb weaver *Leucauge regnyi* (Tetragnathidae) (Simon), that inhabits the Luquillo forest of Puerto Rico, has been observed to build webs of varying angles (vertical-horizontal) in habitats ranging from treefall gaps to forests with dense canopies (Bishop, pers. obs.). Consequently, information on the web building behavior and ecology of this species might contribute to our understanding of the thermoregulatory implications of web angle and the prey availability patterns of the forest ecosystems inhabited by horizontal orb-weavers. This study attempts to investigate what factors affect the angle of the orb webs of *L. regnyi*. We will test two specific hypotheses: 1) the angle of the web of *L. regnyi* is a behavioral thermoregulatory response, and 2) the angle of the webs of *L. regnyi* maximizes prey capture.

METHODS

Study Site.—During June 1991, we studied *Leucauge regnyi* at the El Verde field station in the Luquillo Experimental Forest of Puerto Rico, a tropical tabonuco forest (Brown et al. 1983).

Hypothesis 1: Thermoregulation.—We tested Hypothesis 1 in edge microhabitats where sunlight exposure is greatest and thermoregulatory mechanisms should be most pronounced. We measured the angles, in degrees of departure from vertical, of 200 webs using a clinometer (Suunto PM-5/360 PC). Webs were measured where the lowest value could be obtained, i.e., along the line on which the web was most vertical. When webs were not strictly planar, we used the mean of the web slant above (n = 1) and below (n = 1) the hub. We recorded the compass direction of the sun in the morning (1000 h) and the afternoon (1500 h). We also recorded the direction faced by the side of each web on which the spider rested. We measured the smallest angle between the direction faced by each web and each of the compass directions of the sun, respectively, yielding two values, a morning and afternoon directional angle, each between 0° and 180°, for each of the 200 webs. These values represented the web's orientation relative to the sun, and they were examined for correlations with the angle of the spider webs.

Hypothesis 2: Prey Capture Efficiency.—We collected prey capture data at three sites of varying levels of disturbance due to the passage of Hurricane Hugo (1989) through the forest. These areas of varying disturbance expose the spiders to differences in prey availability due to changes in forest structure among the sites (Bishop, pers. obs.). The high degree of variability among the sites should provide a rigorous test of the hypothesis: despite habitat type, the angle of the web maximizes prey capture in this forest ecosystem. The three sites used in this study were the following — *Least disturbance (Site 1):* Most of the canopy-level trees were left standing after the hurricane, but with foliage and many branches damaged. By June 1991, the canopy was growing back. Because this area was relatively undisturbed, the understory remained relatively open. *Intermediate disturbance (Site 2):* This site was characterized by many fallen trees and branches, and dense successional growth (primarily *Cecropia*) generally 4–6 m tall. *Most disturbance (Site 3):* This site was in a treefall gap with very dense plant debris on the forest floor. In June 1991, successional growth was short (< 3 m).

All prey capture data were collected using sticky traps, consisting of embroidery hoops 25 cm in diameter and covered on both sides with cheese cloth and pest glue (Stickem Special, R. Seabright Industries, Emeryville, California) and placed approximately 1.5 m off the ground. Traps were generally hung on the branches of saplings or on dead, fallen trees. First, in order to determine whether we would need to separate data from traps of varying directional orientation in testing Hypothesis 2 (Castillo & Eberhard 1983), we placed nine traps facing North/South and nine facing East/West and counted the prey inter-

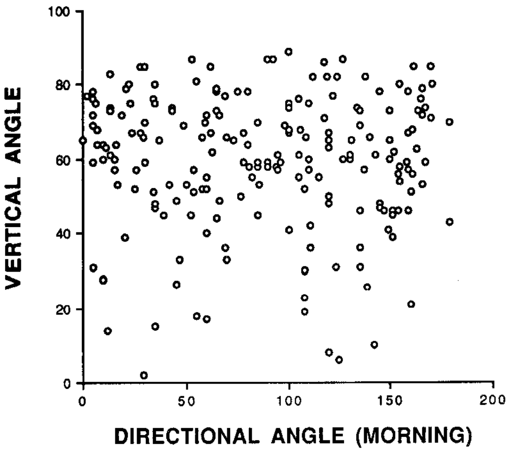

Figure 1.—Scattergram for the directional angle relative to the morning sun (1000 h) and vertical angle of the orb webs of *Leucauge regnyi* (n = 200) in the Luquillo Experimental Forest of Puerto Rico. No correlation was found (r^2 = 0.001, $p > 0.05$), so the equation and line are not shown. Measurements are in degrees.

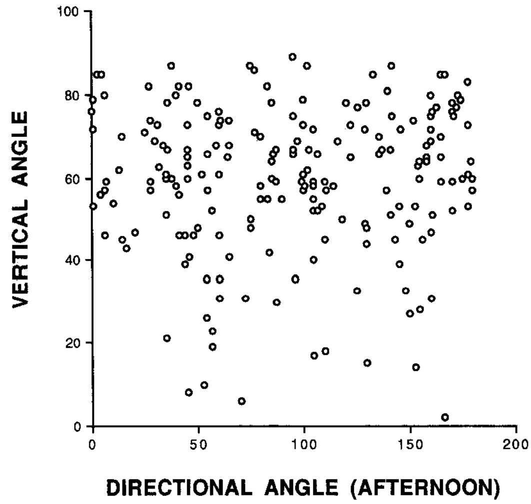

Figure 2.—Scattergram for the directional angle relative to the afternoon sun (1500 h) and vertical angle of the orb webs of *Leucauge regnyi* (n = 200) in the Luquillo Experimental Forest of Puerto Rico. No correlation was found (r^2 = 0.001, $p > 0.05$), so the equation and line are not shown. Measurements are in degrees.

cepted during a 24 h period. The results were analyzed for significant differences using a G-test (Sokal & Rohlf 1987).

We then used sticky traps to test prey availability at each of the three disturbance sites. We positioned eight traps suspended by wire from the vegetation at each of three orientations for a 72 h period to determine prey availability: vertical, horizontal, and the mean angle of the actual webs of *Leucauge regnyi* at that site. We chose a three day sampling period to minimize error due to variation in prey availability caused by daily differences in weather or other periodical parameters, and we interspersed traps of different orientations within an area of approximately 20 m^2.

The mean angle orientation was determined from measurements of 50 web (all adult females) angles at each site, according to the equation for means from a normal distribution given by Krebs (1989). Mean angles at the sites were 55.5°, 63.6°, and 60.5° for sites 1, 2 and 3, respectively and variation among the means was significant (one-factor ANOVA; $F = 3.518$, $P = 0.032$). Fisher's test indicates that only the difference between sites 1 and 2 was significant.

We counted the insects captured on each trap and used G-tests to determine if there were significant differences in the number of prey captured at each of the three sticky trap angles at each site. Multiple G-tests were used to allow testing among specific orientations, so only highly significant results ($P < 0.01$) were accepted.

RESULTS

Thermoregulation.— The direction of the morning sun relative to web orientation was measured at 95° at 1000 h on 22 June 1991, and the direction of the afternoon sun was measured at 290° at 1500 h on the same day. Web orientation relative to the sun ranged from 0° to 180° in both the morning and afternoon with no clear modal value. Web angles varied between 0° and 90°, with a mean of 59° (SD = 17.86, n = 200 webs). We found no correlation between web position relative to the sun and the angle of the webs in the morning or afternoon (morning: r^2 = 0.001, $p >> 0.05$, n = 200; afternoon: r^2 = 0.001, $P >> 0.05$, n = 200) (Figs. 1, 2).

Prey capture.—We found no significant differences in the number of insects captured by North/South versus East/West facing sticky traps (G-test: G_{adj} = 0.007, $P > 0.9$), so we did not separate sticky traps by direction for sampling at the three sites.

At Site 1 (least disturbance), horizontal traps caught significantly more prey than vertical traps (G-test: G_{adj} = 43.118, $P < 0.001$), and mean angle traps caught significantly more prey than vertical traps (G_{adj} = 167.413, $P < 0.001$) and

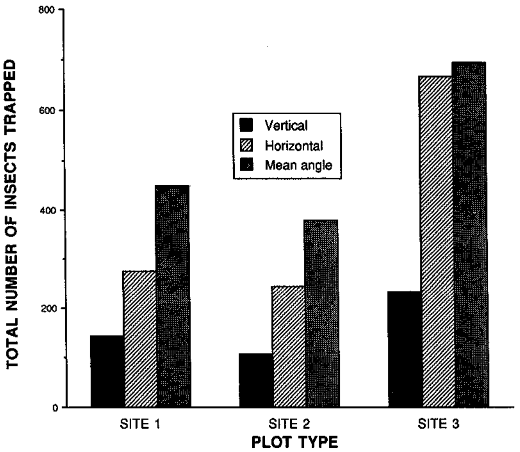

Figure 3.—Comparison of the total numbers of insects caught by vertical, horizontal, and mean angle sticky traps in three different plot types in the Luquillo Experimental Forest of Puerto Rico. The mean angle was determined by measuring the angles of 50 webs of *Leucauge regnyi* at each site and calculating the means of those webs (55.5°, 63.6°, and 60.5° for sites 1, 2 and 3, respectively). Horizontal and mean angle traps caught significantly more prey than vertical traps at all three sites (*G*-test: $p < 0.001$ in each case). Mean angle traps caught significantly more prey than horizontal traps at sites 1 and 2 (*G*-test: $p < 0.001$), but there were no significant differences between the numbers of prey caught by horizontal and mean angle traps at site 3 ($p > 0.1$).

horizontal traps ($G_{adj} = 42.200, P < 0.001$). Likewise, at Site 2 (intermediate disturbance), horizontal traps caught significantly more prey than vertical traps ($G_{adj} = 55.839$, $P < 0.001$), and mean angle traps caught significantly more prey than vertical traps ($G_{adj} = 161.970$, $P < 0.001$) and horizontal traps ($G_{adj} = 29.073$, $P < 0.001$). At site 3 (most disturbance), horizontal traps again caught significantly more prey than vertical traps ($G_{adj} = 216.558$, $P < 0.001$), and mean angle traps caught significantly more prey than vertical traps ($G_{adj} = 239.659$, $P < 0.001$), but there was no significant difference between horizontal and mean angle traps, although mean angle traps caught slightly more prey ($G_{adj} = 0.619$, $P > 0.1$) (Fig. 3).

DISCUSSION

These results suggest that the web angle of *Leucauge regnyi* maximizes the web's prey capture efficiency and is not influenced by the orientation of the web relative to the sun. This does not necessarily mean that thermoregulation exerts no influence on web angle. For example, Krakauer (1972) has argued that web angle may facilitate postural thermoregulation in *Nephila clavipes*. Because we did not quantify posturing behavior, further research is required before concluding that this facilitation does or does not occur in *L. regnyi*.

The prey capture patterns from our data in a tropical forest contrast with the pattern of the open field studied by Chacon & Eberhard (1980), in which vertical traps caught the most prey and horizontal traps caught the fewest. In our study, vertical sticky traps caught significantly fewer prey than either horizontal or mean angle traps, and neither vertical nor horizontal traps caught more prey than the traps positioned at the mean angle of the spider webs measured. The fact that mean angle traps at the least and intermediate disturbance sites caught significantly more prey than horizontal traps suggests that the advantage of the inclined orientation used by *Leucauge regnyi* may be even greater in these two sites.

The data suggest that insect flight patterns in forest systems differ from those in open fields, as meteorological data on wind movement would imply (Pedgley 1982). Vegetation structure may be partly responsible for this. Forest structure probably allows for more vertical movement of insects, and this would account for results in which horizontal and inclined traps catch more prey relative to vertical traps than in an open field. Because mean angle traps did not catch significantly less prey than horizontal traps at any sites, and in fact caught more at two sites, it is unlikely that this pattern can be attributed exclusively to prey falling from above, as suggested by Eberhard (1990). The smaller horizontal sweep of mean angle traps would result in fewer prey captured if this was the sole explanation (Eberhard 1986). Rather, it appears more likely that mean angle traps interfere with more flight patterns than horizontal traps. It may also be more difficult for insects to see and avoid horizontal and mean angle traps (Craig 1990).

Although the reasons for the differences in prey capture found in this study cannot yet proceed beyond speculation, the results themselves raise significant problems for further research in the web ecology of spiders in forest systems. In light of the apparent greater efficiency of more horizontal orientations in intercepting available prey, the vertical orientation of most forest orb-weavers is surprising. However, before vertical orientations are ascribed wholly to other factors, such as thermal stress (Tolbert 1979; Caine & Heiber 1987) or structure for web building (Eberhard 1988), data on the planar prey availability of the actual prey of both horizontal and vertical orb weavers are needed. To avoid the inaccuracies that sticky traps would bring to such a study, actual webs with spiders would have to be reoriented (Eberhard 1989) and observed during the foraging periods of the spiders studied. Further, data on horizontal and vertical orb weavers found in the same microhabitats would provide informative comparisons.

Although sticky trap data can be used for comparisons and for the evaluation of web characteristics such as vertical angle, drawing conclusions about web ecology from sticky trap data has been treated with skepticism (Castillo & Eberhard 1983; Eberhard 1990), due to the differences in the qualities of sticky traps and orb webs. Most notably, the sticky traps we used are much more visible than orb webs; thus, the frequencies and types of prey caught in our study may be different than those of actual webs. Sticky traps only mimic the encounter function of orb webs and capture potential prey items, not necessarily the actual prey of *Leucauge regnyi*. Furthermore, we did not classify the prey caught in our traps by taxon or size. However, because small dipterans constituted the overwhelming majority of sticky trap captures, and the same group also constitutes most of the diet of *L. regnyi* (Bishop, pers. obs.), and because the data showed an extremely high level of significance ($P < 0.001$ in all instances of significant differences), the general trend may well be biologically significant.

The significant differences in actual spider web angle among the sites may not be solely related to prey capture efficiency, although such a possibility can not be ruled out. Vegetational differences among sites may affect web angle by changing the structure available for web building (Buskirk 1975; Gillespie 1987; Eberhard 1988), or web angle may vary as a response to some unknown parameter. The variation in orientation among forest sites with different structure, along with the implications of the sticky trap results, add to current knowledge of the selective forces acting on spider webs, but the contrast that our findings present with past research further complicates the problem of thoroughly assessing the role of these forces on the evolution and ecology of orb web orientation. Most importantly, they indicate that relevant parameters may vary considerably among ecosystems.

ACKNOWLEDGMENTS

This research was funded by a grant for undergraduate research from the Ford Foundation, awarded through Earlham College to Leslie Bishop. Additional support was provided to Bishop by the Exline-Frizzell Fund of the California Academy of Sciences, and an Oak Ridge Associated Universities Faculty Travel Grant. We would like to express our gratitude to the staff of the El Verde Field Station (Center for Energy and Environmental Research, University of Puerto Rico) for the use of their facilities and for providing access to the tropical study sites. We also thank Ann Rypstra and George Uetz for discussion and suggestions during the planning of this project, and Andrea Condit and Sandra Encalada for assistance in the field. Susan E. Riechert, William Eberhard, and Al Cady provided valuable reviews of the manuscript.

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Manuscript received 24 October 1991, revised 29 August 1992.