TREES AS PROVIDERS OF STRUCTURE, PREY CAPTURE, AND PROTECTION FOR WEB-BUILDING SPIDERS

GABRIEL H. CALVI, TIMOTHY R. MATSUURA AND LAKSHMI NARAYAN

Abstract: Large trees and understory plants provide substrate for web-building spiders. We hypothesized that placement and orientation of spider webs affects the type and abundance of prey captured. We predicted that webs built on the buttresses of large trees would have increased prey capture, debris, and less damage than webs built among smaller understory plants. Using simulated webs and observations of natural spider webs, we tested the benefits of building webs in the buttresses of large trees or among understory plants. There was no difference in prey capture between treatments near or far from trees. We found that spider webs on trees accumulated more debris and experienced less damage. Webs built in the buttresses of trees were more often oriented parallel to the ground than were webs far from a tree. Though we did not quantify the costs and benefits of web placement on large trees and understory plants, location and orientation of webs appears to influence the amount of debris accumulated and damage suffered by a web.

Key Words: Arachnida, buttresses, La Selva, web orientation

INTRODUCTION

Web weaving is a common spider strategy for capturing prey (Kaston 1953). Spider webs differ in both shape and placement. Both large trees and understory plants provide the structure for building webs, but they may have different benefits and costs for spiders that build on them.

The vertical relief of a large tree may increase prey capture in horizontally oriented webs. The sturdy nature of tree buttresses, unlike smaller understory shrubs and saplings, provides protection for spider webs from physical stresses such as rain, wind, and animal disturbance. The cost, however, is that these webs may accumulate debris falling from overhead in the tree. Alternately, webs placed away from the base of large trees, especially those with a vertical orientation, might minimize the amount of debris collected while capturing more mobile prey.

We hypothesized that the location and orientation of webs would affect the type and abundance of prey captured. We predicted that horizontally oriented webs near trees would accumulate more debris and capture larger, less mobile arthropods such as beetles and ants compared to webs in the forest understory. We also predicted that webs away from trees that were vertically oriented would accumulate less debris and capture more flying insects than would webs in the buttresses of trees.

METHODS

To examine the relative effectiveness and taxa-specific catch patterns of differently placed webs, we established experimental webs around buttressed trees approximately 15 m apart on opposite sides of the CES trail at La Selva Biological

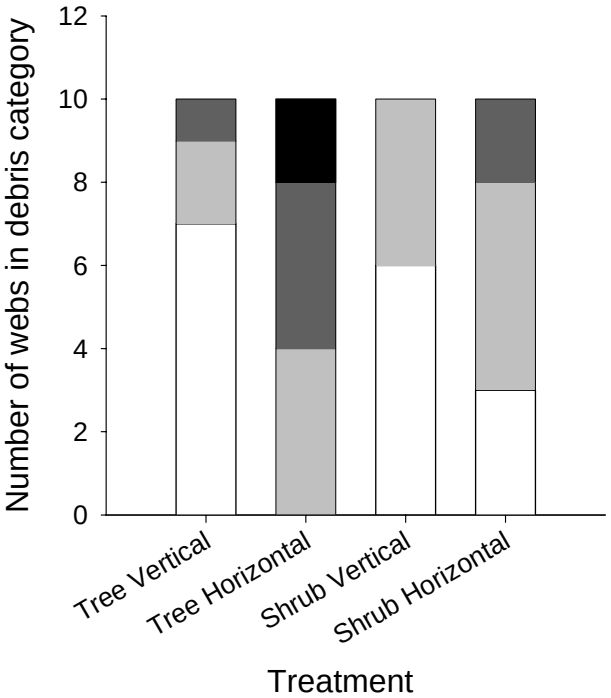

Figure 1. Frequency of different levels of debris in simulated webs, grouped by treatment (substrate type and web orientation). Debris ranges from 1-4, with the lightest bars represent the lowest debris levels (1), and darkest bars highest debris (4). (n = 40).

Station, Costa Rica. We created webs by coating sheets of Ziplock® plastic (each ≈ 18 x 35 cm) with Tanglefoot®, and suspending these traps between 20 and 40 cm above the forest floor. Our four treatments consisted of traps placed horizontally against the tree, vertically against the tree, horizontally approximately 2 m away from the tree on stakes, and vertically 2 m away from the tree on stakes. For each of our 24-h sampling periods (13-14 and 14-15 Feb 2004), we had five replicates of each of our four treatments.

After each 24-h catch period, we counted and identified (to order) all arthropods caught in the experimental webs. We also scored the amount of debris within each web on a scale from 0-4.

We also quantified placement, orientation, damage, and debris collected in naturally occurring spider webs on and around buttressed trees. On 14-15 February 2005, we measured all spider webs encountered on 10 trees and within a 2 m radius of each focal tree, including all webs from the ground up to 2.2 m. We selected focal trees by walking a random number of paces between zero and 100 along the CES, then heading perpendicularly off the trail (randomizing direction) until we encountered a buttressed tree. Our focal trees ranged from 27 to 75 cm in diameter at breast height. For each web present, we recorded the substrate the web was attached to, distance from the ground, web type (three-dimensional or orb), damage on a scale from 0-4, debris on a scale from 0-4, and the presence of any spiders or insects on the web. For all orb webs, we also recorded the angle they made relative to the ground, from 0˚ - 90˚. For the purposes of our analysis, we simplified the substrate variable into two main groups: those attached to our focal tree, and those attached to shrubs and other surrounding objects, heretofore called shrubs.

We used ANOVAs to analyze total and taxa-specific arthropod abundances from our simulated webs. We used an ordinal logistic regression to compare debris level. For observational data, we used contingency analysis to compare web structure, damage, and debris for webs on trees and shrubs. We used a one-way ANOVA to compare angles on trees and shrubs. All data met the assumptions of the statistical tests performed with the exception of the damage and angle measurements in our observational data, which were not nor-

mally distributed. Neither of these data could be normalized using log or square-root transformations.

RESULTS

For the simulated web experiment, we found no effect of substrate, web orientation, or the interaction between these two factors on arthropod abundance (Table 1). Mean insect abundances (± 1 SE) for each treatment were: tree horizontal 10.6 ± 0.9; tree vertical 13.8 ± 3.0; away vertical 9.6 ± 1.9; away horizontal 15.0 ± 3.3. We also tested for effects of substrate, orientation, and an interaction between these factors on the abundance of dipterans, hymenopterans, and coleopterans, the three most abundant arthropod orders in our webs. Our results showed no effect of these variables on arthropod abundance (Table 2.)

The results of an ordinal logistic regression showed that the interaction between substrate and orientation had a significant impact on debris found in the webs (χ^2 = 4.18, df = 1, P = 0.04). Webs placed horizontally against trees had the most debris (Fig. 1).

A logistic ordinal regression of our observational data also showed that debris was greater in spider webs attached to trees (χ^2 = 10.25, df = 4, 125, P = 0.04). A similar analysis on the damage of spider webs showed that webs attached to trees had less damage than those attached to shrubs (χ^2 = 18.16, df = 4, 125, P = 0.001; Table 3).

Analyses of our observational data also showed that shrubs tended to have more orb webs (39) than three dimensional

Table 1. Results of two-way ANOVA tests for the effects of different treatments on arthropod abundance per web. df = 1, 36 for each test (n = 40).

Effect	F	P
Distance	0.00	0.97
Orientation	0.20	0.65
Distance*Orientation	3.12	0.09

Table 2. Results of two-way ANOVA tests for the effects of different variables on abundance of three most abundant arthropod taxa on model webs. df = 1, 36 for all tests. (n = 40).

Order	Mean abundance per web	Effect	F	P
Diptera	8.80			
		Distance	0.22	0.64
		Orientation	0.46	0.50
		Distance*Orientation	1.95	0.17
Hymenoptera	1.33			
		Distance	2.62	0.11
		Orientation	0.01	0.94
		Distance*Orientation	1.00	0.32
Hymenoptera	1.33			
		Distance	0.26	0.61
		Orientation	0.00	1.00
		Distance*Orientation	0.26	0.61

Table 3. Number of webs with different debris and damage levels (0-4) in trees vs shrubs (n = 133).

	Debris					Damage				
Level	0	1	2	3	4	0	1	2	3	4
Shrub	18	25	4	2	0	14	10	12	9	4
Tree	17	38	23	4	2	46	21	12	5	0

webs (10), while webs on trees were evenly distributed between the two types (43 three dimensional webs and 41 orb webs; χ^2= 10.56, df = 1, 131, P = 0.01). The orb webs we found had a higher angle of orientation on shrubs than on trees, with a mean angle of 43.3 ± 5.8° on shrubs compared to 23.1 ± 5.4° on trees (F = 6.55, df = 1, 81, P = 0.01).

DISCUSSION

Though webs on buttresses had more debris than webs in shrubs, our results indicate that spider webs on trees had less damage than webs suspended in shrubs. We also found that horizontally oriented webs caught more debris than vertically oriented webs, and webs that were placed horizontally between buttresses had the greatest levels of debris. The trees and their epiphytes probably provide the source of this debris, but it is unclear how this affects spiders. Increased debris capture may be costly if it damages webs or makes them more visible to predators or prey, but it may be beneficial if increased falling debris is positively correlated with the abundance of falling prey.

Our observational results showed that webs close to trees tended to be positioned at lower angles than webs on shrubs. Since we also observed webs positioned vertically on trees, the differential orientation of webs on trees versus shrubs may be a strategic tradeoff rather than a result of structural limitations. If increased debris catch from horizontal placement were detrimental to spiders, they could both gain protection and minimize damage due to falling debris by building vertically positioned webs close to trees. The prevalence of horizontal webs on trees suggests that some spiders may benefit in some way that outweighs the costs of debris catch, or debris catch may actually benefit spiders by attracting prey that use debris as a food or habitat resource. Also, web destruction, a presumed cost of debris capture, may not affect all spiders equally, as webs of many spider species are ephemeral, lasting no longer than one day (Goodwin 1997).

Contrary to our predictions, our manipulative experiment showed no effect of web orientation or proximity to tree on either the amount or type of prey caught in webs; however, this result may have resulted from methodological constraints, as our sticky traps were unable to catch large insects. We observed large coleopterans crawling off of our traps, and could not determine how the type of prey we were able to catch compared to that caught in real webs. Additionally, overall low prey numbers in real webs that we observed prevented us from quantifying differences in prey capture between real and simulated webs.

Our results also showed differences

in the type of webs placed on shrubs and trees. This could be the result of a structural constraint that limits the ability of spiders to build three dimensional webs on shrubs. However, we observed both types of webs on each substrate, but proportionally more orb webs on shrubs. Additionally, webs tended to be oriented more vertically on shrubs than trees. That web type and angle of placement differ between placement sites suggests that different prey capture strategies may be more effective in different locations. Substrate clearly affects the form and orientation of spider webs, and further studies of building patterns could lead to a better understanding of the effects of site selection and orientation on damage and prey capture efficiency of spider webs.

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Circadian foraging patterns in *Paraponera clavata*

Jonathon C. Raffensperger

Abstract: Paraponera clavata is a large ponerine ant that feeds on nectar and insects in the understory of tropical forests. Although foraging activity of this ant has been shown to be higher at night than during the day, the mechanism behind this increased rate is unclear. I predicted that individual workers would forage both day and night, becoming more active after dark, and that insect abundance and activity would he higher at night, resulting in a larger percentage of insects in the food brought back to the nest. While I found no difference in the percent composition of food by day versus night, it appears from observations of individually marked ants that daytime workers do remain active and increase their foraging rate at night, but are also joined by a group of exclusively nocturnal foragers.

Key Words: ant foraging, food availability, giant tropical ant, nectar, social organization

Introduction

The giant tropical ant, *Paraponera clavata*, is a common understory forager in the Atlantic coastal lowlands of Costa Rica whose nests are constructed at the bases of large trees and house colonies of 700 to 1,400 workers. This species has been observed to be most active at night, although some workers can be found on foliage and tree trunks during daylight hours (Janzen and Carroll 1983). It is not known, however, whether this nocturnal increase in activity is the result of a general increase in foraging rate, or whether there is some division of labor among workers between day and night, with a larger "night shift" taking over once the sun goes down. Be-