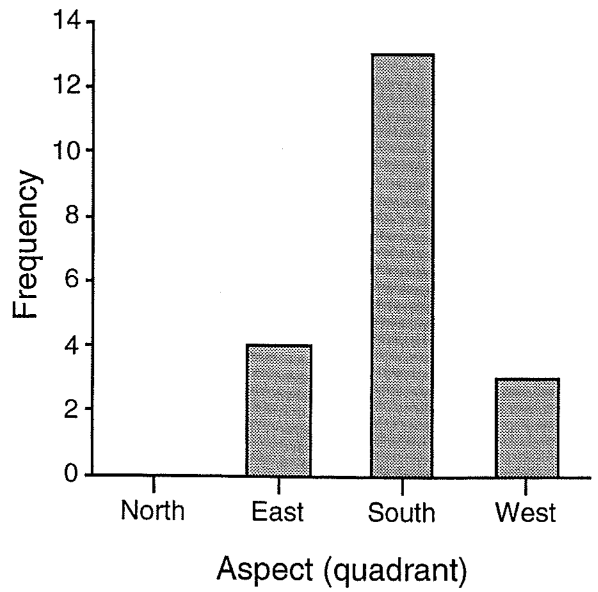
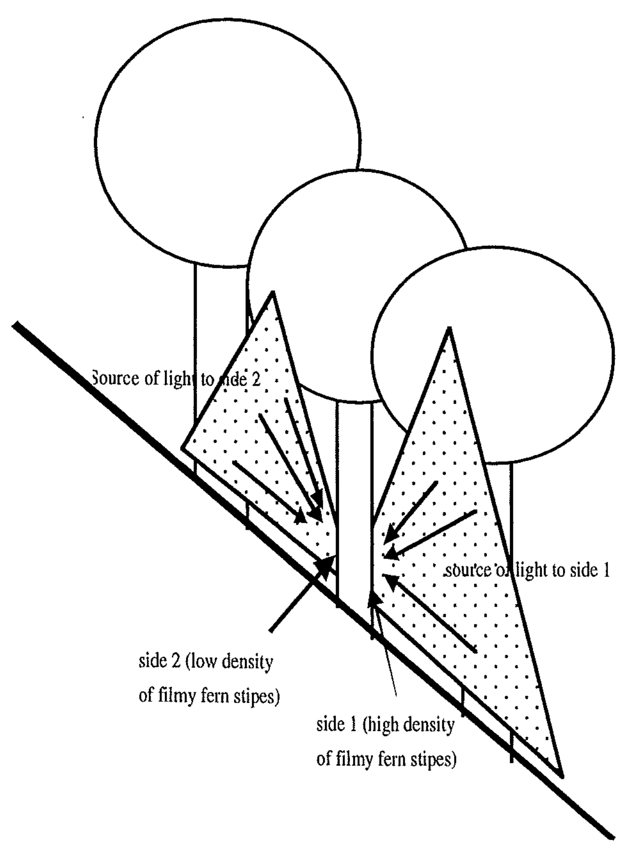


FIG. 1. Frequency with which the area of maximum *H. asplenoides* abundance on a tree trunk faces each of the four cardinal directions (90° sectors; n = 20).

FIG. 2. There is probably greater light exposure to the side of a tree trunk facing downhill.



Discussion

We found a significantly greater density of *H. asplenoides* on the steep, downhill (south) side of trees. Although we subjectively perceived greater light exposure on the downhill side of the tree, there was no correlation between fern density and canopy cover. In retrospect, we realize that a horizontally– oriented spherical densiometer would not capture relevant differences in light exposure on near-vertical tree trunk surfaces (Fig. 2). Measuring light exposure with a properly oriented light meter or spherical densiometer would allow a better assessment of light associations and may provide further insight into why *H. asplenoides* is most abundant on the downhill side of trees.

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Microhabitat selection by orb-weaving spiders in a montane cloud forest

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Abstract: A spider's choice of web location may be influenced by a variety of microhabitat elements including food availability, probability of web damage, predation risk, thermal environment, and distribution of preferred prey. We predicted that web location of orb-weaving spiders in the tropical cloud forest at Monteverde, Costa Rica, would be strongly affected by prey capture and risk of web damage. We did find more webs in areas protected from wind, but the mean damage index was only slightly lower than in more exposed sites. Using insect traps, we found that prey availability was equal in exposed and protected areas. Since prey capture and web damage did not adequately predict web location, other factors such as predation, microclimate and prey preference may exert a stronger influence on web placement.

Key Words: Arachnida, *cost and benefit trade-offs, prey capture, web damage*

Introduction

Microhabitat selection is important to organisms because the advantages of a favorable microhabitat can profoundly enhance their growth, survival, and reproductive success. The microhabitat selected by an individual spider is especially important as it serves as both a living space and a foraging site. Presumably, natural selection favors spiders that build webs in microhabitats where overall benefits are maximized. However, there are costs associated with seeking out optimal locations. These include the energetic and material costs of finding suitable sites and building new webs.

Orb-weaving spiders of the family Araneidae have evolved mechanisms to reduce these costs by recycling their silk. Therefore, orb-weavers can explore a variety of potential web locations at minimal cost. This capability provides greater flexibility to build webs in the most favorable microhabitats despite frequently changing conditions. A spider's choice of web location may depend on a variety of potentially conflicting microhabitat attributes including food availability, probability of web damage, predation risk, thermal environment, and distribution of preferred prey. In a montane cloud forest, these variables might fluctuate daily. Therefore, a spider's behavior reflects a compromise between the needs and selection pressures influencing the spider at that point in time (Reichert and Gillespie 1986). We focused on how prey availability and web damage affect web placement in orb-weaving spiders. We predicted that spiders would choose to occupy protected rather than exposed sites, because webs in protected locations would maximize prey capture and minimize web damage.

Methods

We conducted this study on 21-22 January 2003 in Monteverde, Puntarenas Province, Costa Rica, along the Sendero Resbalon and Sendero Jilguero near La Estación Biológica. Between the hours of 07:55 and 10:15, we surveyed the first 50 orb-weaver webs we saw within 1 m of the trail. For each web, we recorded location (exposed/protected), orb length, width, and height above nearest substrate. Protected sites were within 15 cm of the substrate below and fully sheltered on at least one side. These sites were in locations such as under a log, between tree buttresses, or in a hillside alcove. Exposed sites were located in open areas, without nearby protection from wind and usually occurred in the vegetation more than 15 cm from the substrate below. We also determined the amount of damage on each web using a scale of 0-3 (where 0 = no damage, 1 = 1 - 10% damage, 2 = 10 - 20% damage and 3 = > 20% damage).

We conducted field experiments to measure prey availability in exposed and protected sites. We averaged the dimensions of the surveyed webs and constructed insect traps from sheets of acetate according to those dimensions (14.0 x 10.5 cm). We than applied Tanglefoot™ insect trap coating to the traps. Six sites were haphazardly chosen and two traps were placed at each site, one in a protected area and the other in an exposed area, for a total of 12 webs. We attempted to place our traps in orientations similar to those of natural webs. We collected the traps after 24 h and counted the number of insects captured on each. The number of insects captured was averaged for both the exposed and the protected traps. Because almost all of the insects were less than 3 mm in length, we were not able to measure biomass. We used one-way ANOVA to determine whether the number of prey captured was significantly different between the two treatments.

Results

Of the 50 orb-weaving spider webs that we surveyed, 18 were in exposed sites and 32 were in protected locations. Exposed webs were more damaged than protected, but this difference was only marginally significant (Fig. 1; F = 3.53, df = 48, P = 0.07).

Traps in exposed and protected locations captured similar numbers of insects. Prey capture for exposed webs was 5.0 ± 0.86 (mean ± SE) while the average for protected webs was 4.8 ± 1.40, and this difference was not significant (F = 0.01, df = 10, P = 0.92).

Discussion

Our findings support the hypothesis that microhabitat influences web location in orb-weaving spiders. Spiders in the Monteverde cloud forest appear to choose protected sites. However, the factors that

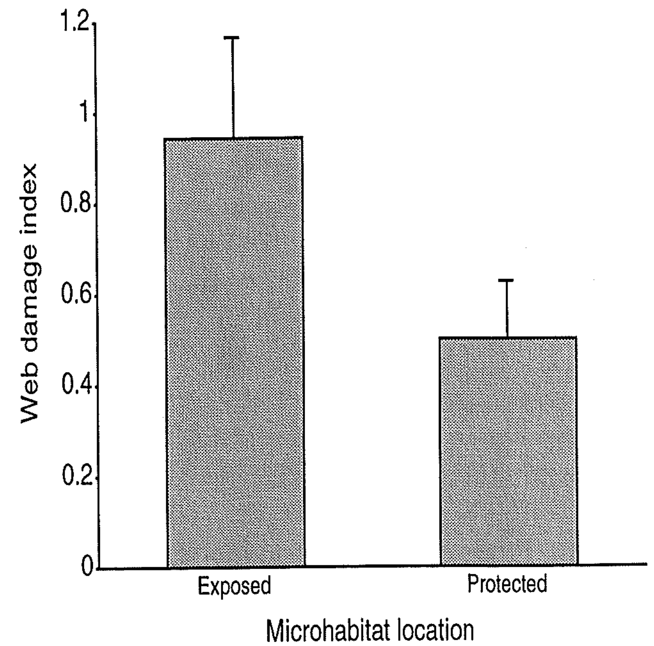

FIG. 1. Mean damage (scaled from 0 - 3) to orb-weaving spider webs in wind-exposed (n = 18) and protected sites (n = 32) at Monteverde, Costa Rica. Values are means ± S.E.

we examined—web damage and food supply—do not adequately explain this pattern. Although the trend of increased damage in exposed sites may have important biological implications, it was only marginally significant statistically. Furthermore, based on our experimental data, prey abundance did not differ between protected and exposed sites, implying that other factors contribute to the apparent preference for protected sites.

Predator avoidance, although largely unstudied, could be an important factor in determining web location. Since spiders must remain in the vicinity of their webs to monitor prey capture, exposed webs may be more conspicuous to predators. This idea is supported by the observation that some spiders camouflage themselves by building webs near tree bark where they may be more cryptic (Curtis and Morton, 1974; Robinson and Lubin 1979; Robinson 1982).

Microclimate may also play a role in web site location. According to Savory (1971), spiders are restricted by desiccation stress to favorable thermal environments. In

general, we observed that the webs located in exposed areas received more sunlight than those in protected sites. Additionally, protected webs were located close to the ground, in cool, moist microhabitats. Perhaps protected areas with minimal exposure to direct sunlight reduce desiccation, especially on warm, sunny days. The degree to which water loss affects spiders in montane cloud forests is unknown.

Finally, the distribution of specific, preferred prey may exert a strong influence on web site selection. Prey-type may be more important than prey quantity, but our trap data were limited to total prey abundance.

The choice of where to build a web represents a compromise between conflicting forces. Future studies could examine the interactions between prey availability, prey type, web damage, predation, and microclimate to determine which factors most strongly influence web location. Studies over a longer time scale are also needed to account for daily variations in environmental factors. We sampled on only one relatively mild day. On a windy day, webs may have suffered more extensive damage. Since orb weavers are able to change web location frequently, they can readily adjust to daily fluctuations in microhabitat conditions. The tendency to build webs in protected areas may be influenced by the particular conditions prevailing at the time we sampled.

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