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THE WEB OF *NUCTENEA SCLOPETARIA* (ARANEAE, ARANEIDAE): RELATIONSHIP BETWEEN BODY SIZE AND WEB DESIGN

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ABSTRACT. The relationship between body size and web design was studied for the nocturnal orb-weaving spider *Nuctenea sclopetaria*. Body measurements (carapace width, leg length, body length and wet weight) taken from 27 adult female and 22 juvenile spiders were related to web dimensions (capture area, number of radii, capture thread length, mesh height) each spider constructed. Carapace width was found to be the most reliable size measure for predicting web dimensions for adult and juvenile spiders. The study also found that the webs showed a distinct asymmetry due to the enlargement of the lower web half and the extent of this asymmetry increased with carapace width. Furthermore, mesh height increased with distance from the hub. The possible effects of web asymmetry on the prey capture success of spiders are discussed.

The webs of orb-web weaving spiders show great variations in their specific designs (see Eberhard 1986 for a summary) which have been interpreted as specializations for the capture of specific prey types (e.g., Eberhard 1980, 1986; Brown 1981; Murakami 1983; Craig 1987b, c; Walker 1992; Rhisiart & Vollrath 1993; Miyashita & Shinkai 1995). Orb web design can also vary between individuals of the same species and even within individuals in response to prey size (Sandoval 1994), food availability, egg production (Sherman 1994), web site and spider size (Eberhard 1988). Within species, web design (e.g., web size and mesh size) can relate to various measures of body size such as spider length (Waldorf 1976; Brown 1981), carapace width (Olive 1980; Murakami 1983; Eberhard 1988), leg length and spider weight (Eberhard 1988) but other studies have not found such relationship between spider size and web design (Leborgne & Pasquet 1987). Similarly, not all body dimensions may be equally relevant to web design. The body size of spiders can change quite drastically within a short period of time during the ingestion of large prey and during a molt (Vollrath & Köhler 1996). While the accumulation of energy reserves through foraging influences the molt and the increase in body size after the molt, prey ingestion also affects body weight immediately and directly (Vollrath 1987a). Thus, spider weight is also an indicator of the spider's satiation level that directly influences web investment and consequently web design (Sherman 1994).

Furthermore, in an adult spider that has undergone its final molt, spider weight reflects the recent foraging success as well as the cumulative foraging success between molts. In contrast, body size characteristics such as leg length or carapace size reflect the foraging success prior to the final molt but are no longer influenced by the prey captured after the final molt (Vollrath 1987a; 1988). Leg length can also be misleading as autonomized legs regenerate shorter than normal legs (Vollrath 1987b). Consequently, various body size measures may have different significance in relation to web design depending on whether the spider is juvenile and still undergoing molts or whether it is adult. In addition to inter- and intraspecific differences in web design, webs are not necessarily symmetrical, and various web elements can be differentially allocated in the top half compared to the bottom half of the web. An example of such web asymmetry is the ladder web built by *Kryptaraneus atrihastulus* (Urquhart 1891) with extreme up or down extensions of the orb (Forster & Forster 1985).

The objective of the present study is to describe the variation of orb web design, using the webs of *Nuctenea sclopetaria* (Clerck 1757). This species of nocturnal orb weavers is common in urban habitats and often found in high densities near water (Wasowska 1973). By relating a number of different body size measures to various web characteristics we aim to identify useful size measures for both adult and juvenile spiders and to describe the relationship between spider size and web design in comparison with previous studies. Furthermore, we describe the nature of web asymmetry in this species and reveal how various web elements are differentially allocated. Voucher specimens of this species were deposited in the Arachnoidea collection at the Natural History Museum, Vienna, Austria.

METHODS

The material for this study was collected from a footbridge (length = 59 m) across the Danubian Channel in the 9th Vienna district, Austria. *Nuctenea sclopetaria* builds webs near the fluorescent lighting tubes affixed to the top of the handrails (height = 1.31 m) on the footbridge. Observations were made from July until late September 1995, in the evening, after the lights had been switched on. The 27 adult female and 22 spiders (of unidentifiable sex) were selected randomly, and their web and body dimensions were examined. Spiders were removed from their webs and taken to the laboratory where they were weighed to the nearest 0.1 mg on an electronic balance. Carapace width, body length and length of the first right leg (tarsus to coxa) were measured to the nearest 0.01 mm, using a binocular microscope equipped with a Wild Censor.

After the removal of spiders, webs were sprayed with a fine mist of water (Stowe 1978) and cornstarch (Carico 1977) to improve resolution, backlit and photographed using high contrast black and white film. All web parameters were measured directly from these photographs. On the web surface with a clockwise oriented capture spiral, the northern and southern cardinal sectors were defined as the vertically directed sectors above and below the hub, respectively and the eastern and western cardinal sectors were defined as the horizontally directed sectors on the right and on the left hand side of the hub, respectively (Fig. 1). The total capture thread length, as a measure of web investment was obtained by tracing and measuring the length of each spiral thread in the web. The total area covered by the sticky spirals (capture area) was calculated using various web parameters. The total number of radii in the web was counted. The number of capture thread rounds and the length of each radius were obtained for each of the cardinal sectors (north, east, south and west; see Fig. 1). The average mesh height in the webs was calculated from the distances between the capture threads in the vertical directed sectors. Each distance between the spirals in the southern-directed sector of the web (Fig. 1) was also measured in relation to its distance to the hub.

Statistical analyses.—As all data were normally distributed (Kolmogorov-Smirnov), parametric tests were applied. The relationships of all body size measures (carapace width, leg length, body length and wet weight) to capture thread length, number of radii, mesh height and capture area were calculated using Pearson correlations, treating adult females and juveniles separately. To investigate the asymmetric nature of the webs built by adult female spiders, radii length and number of capture threads were compared between the eastern and western sector as well as between the northern and southern sectors using paired *t*-tests as web measures were not independent. The differences between the upper and lower web halves (northern and southern sectors) were further analyzed comparing the capture thread length, the number of radii, the mesh height and the capture area (Fig. 1) using paired *t*-tests.

Web asymmetry was defined as the absolute difference in the number of capture thread rounds between the upper and lower vertical radius. It was related to spider size using regression analysis, pooling the data of adult female and juvenile webs. The relationship between mesh height measured in the southern sector (Fig. 1) and the distance from the hub to the relating mesh in the webs of adult females was investigated using Spearman rank correlations.

RESULTS

In adult females, capture area increased significantly with carapace width and capture thread length increased significantly with carapace width and wet weight, while leg length and body length did not relate to these two

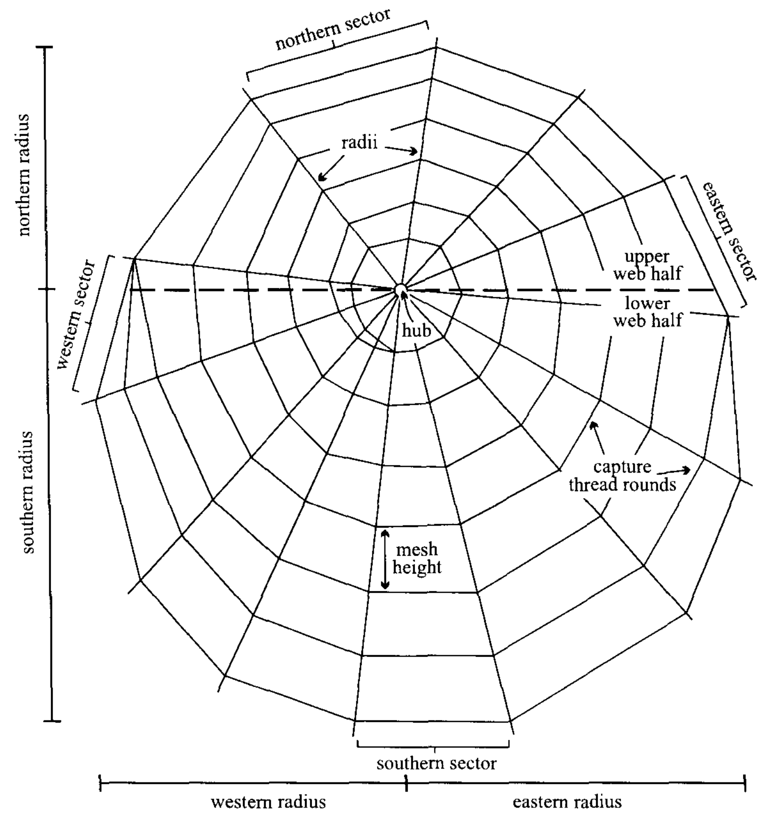

Figure 1.—Schematic orb web, representing the measured parameters.

web variables (Table 1). The number of radii and the mesh height in the webs of adults females did not correlate with any of the four different body size measures of the spiders. In contrast, all body measures, taken from juveniles, were significantly positively correlated with capture thread length, capture area and mesh height (Table 1). As for the webs of adult spiders, there was also no correlation between any of the body measures and the number of radii in the webs of juveniles (Table 1) and the mean (± SD) number of radii did not differ between the webs of adult females (18 ± 2.2) and juveniles (17.9 ± 2.7).

The comparison of the number of capture thread rounds and radii length in the four cardinal sectors of the webs (Fig. 2) revealed that the eastern and western sectors did not differ significantly ($t = -0.73$, $df = 26$, $P > 0.05$; $t = -0.42$, $df = 26$, $P > 0.05$, respectively), but the northern and southern sectors did (number of capture thread rounds: $t = -9.06$,

Table 1.—The correlation coefficients (r) for body- and web measures of adult female ($n = 29$) and juvenile ($n = 22$) *Nuctenea sclopetaria* (* $P < 0.05$; ** $P < 0.01$).

	Capture area (mm^2)		Capture thread length (mm)		Number of radii		Mesh height (mm)	
	Female	Juvenile	Female	Juvenile	Female	Juvenile	Female	Juvenile
Carapace width	0.48**	0.8**	0.42*	0.68**	0.03	−0.12	0.15	0.61**
Leg length	0.29	0.7**	0.36	0.63**	0.03	−0.19	0.064	0.53**
Body length	−0.08	0.66**	0.03	0.58**	0.07	−0.21	−0.23	0.48*
Wet weight	0.25	0.74**	0.38*	0.62**	0.06	−0.09	−0.02	0.47*

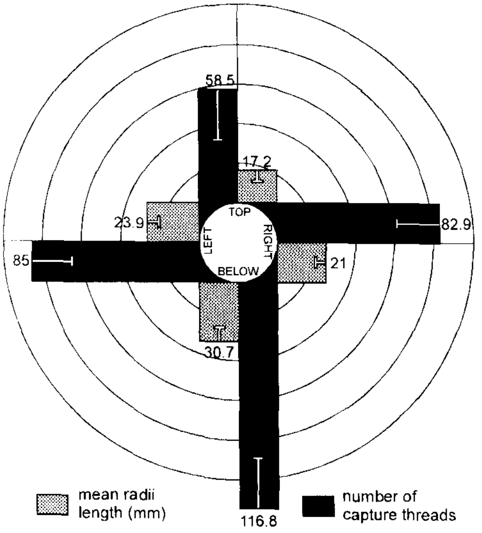

Figure 2.—Mean radii length from the hub to the outermost spiral (mm, black bars), and number of capture threads (gray bars) in the four cardinal directions in webs of adult female *Nuctenea sclopetaria*. Only one SD bar was drawn to simplify the graph. Interval of concentric lines: 20 mm or 20 capture threads, respectively (n = 27).

df = 26, $P < 0.001$; radii lengths: $t = -11.9$, df = 26, $P < 0.001$). Comparisons of more web elements between the upper (northern) and lower (southern) web half revealed further differences. The lower web half contains a significantly longer capture thread, significantly more radii and has a significantly larger capture area than the upper web half (Table 2).

The degree of web asymmetry, defined as the absolute difference in the number of capture thread rounds between the northern and the southern radius, was not constant. It increased significantly with carapace width ($y = 0.982 \times 10$^(0.24x); $R^2 = 0.374$, df = 47, $P < 0.001$). Similarly, the distances between the capture spirals (measured in the southern sector only) were also not constant throughout the sector, but increased significantly with distance from the hub ($r = 0.6735$, df = 26; $P < 0.001$).

DISCUSSION

The web design in adult spiders related differently to the various body size measures. Only capture area and capture thread length increased with carapace width, in accordance with previous studies that also found a positive relationship between carapace width and web size (Olive 1980; Murakami 1983; Eberhard 1988). Interestingly, capture thread length also increased with spider weight. This is surprising, as heavier spiders are presumably more satiated or close to producing a cocoon and are thus expected to decrease their foraging effort expressed by capture thread length (Sherman 1994). It may be that in our spiders wet weight reflected the overall size of the spider more accurately and not so much the recent prey ingestion and thus satiation.

Mesh height did not relate to any of the body size measures for adult spiders, contrasting the results other studies that found leg length a good indicator of mesh height (Vollrath 1987b; Eberhard 1988). However, mesh height can be variable and spiders may alter it independent of spider size to target specifically sized prey (Sandoval 1994). The prey captured by the population of *N. sclopetaria* in our study almost exclusively consisted of small (2.7 ± 0.7 mm body length) chironomid flies, and the mesh height in their webs may be more related to the available prey size than leg length. In contrast to adult spiders, capture area, capture thread length and mesh height related to all body size measures of juvenile spiders, suggesting that size in juveniles has different impacts on web design compared to adults. Consequently, for comparisons between adults and juveniles, carapace width

Table 2.—Web characteristics of adult female *Nuctenea sclopetaria*. Capture thread length, number of radii and capture area differed significantly between the upper and the lower web half. All figures are Mean ± SD (n = 27; *** $P < 0.001$).

	Upper web half	Lower web half	t
Capture thread length (mm)	3944 ± 1389	7524 ± 1905	12.88***
Number of radii	7.7 ± 1.1	10.3 ± 1.6	7.59***
Capture area (mm^2)	14680 ± 5760	26676 ± 9141	10.34***

seems to be the most appropriate variable to indicate the effect of body size on web design.

The number of radii in the web did not correlate with body size in either adult or juvenile spiders. This pattern could be attributed to a number of causes. Non-sticky radii function to stabilize the orb-web; and, consequently, there may be a minimum number of radii necessary for web construction. Radii-rich webs have also been shown to absorb more kinetic energy and are therefore proposed as adaptations to heavier and/or faster flying prey (Craig 1987a; Eberhard 1990). Additionally, larger spiders may increase web stability by increasing the diameter of their silk as an isometric function of spider size (Craig 1987a), rather than by constructing more radii.

The present results reveal a very characteristic asymmetry in the webs of adult female *N. sclopetaria.* While the left and right sides of the web are similar, significantly more material was invested in the lower web half than in the upper half. Like most orb-web spiders, *N. sclopetaria* starts attacking prey from the hub of the web, hanging head downwards. By placing the hub above the center of the web, prey capture success of *N. sclopetaria* can be enhanced, as the time taken to reach prey entangled in the lower half is shorter than in the upper one (Masters & Moffat 1983). Similarly, by hanging head downwards the spider locates prey in the lower half of the web faster than in the upper half (Klärner & Barth 1982) which may lead to an increased prey capture success. Consequently, there may be a selection for asymmetric webs with an emphasis on the lower web half in vertical orb-webs.

Interestingly, web asymmetry increased with body size. Whereas there is room for variation in web design that can change within an individual nightly (Sherman 1994), the general web architecture is thought to be genetically determined and therefore not influenced by individual experience (Foelix 1992). Therefore, web asymmetry may be an indicator for changes in web structure due to previous experience, which in turn increases prey capture success.

Nuctenea sclopetaria places the capture spiral in a way that the distance between consecutive spirals (mesh height) increases significantly with distance from the hub. This may reflect a strategy to optimize the prey capture efficiency of the web. The closer to the hub the prey is retained, the faster it can be reached and subdued by the spider. If the prey is entangled further from the hub, it may have a higher chance of escape (Rhisiart & Vollrath 1993). Consequently, the capture threads near the hub are most important and thus the investment of sticky material should decrease with increasing distance from the hub. This phenomenon has already been observed for the webs of *Araneus diadematus* (Clerck 1757) (Nentwig 1983; Vollrath 1987). The present study found carapace width to be the most reliable predictor of web dimensions for adult and juvenile *Nuctenea sclopetaria* and supports the use of carapace width in future studies concerned with relationship of body size to web dimensions.

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