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Does mesh height influence prey length in orb-web spiders (Araneae)?

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Abstract. The relationship between web design and prey capture in orb-web spiders was examined by correlating the mean mesh height with the mean prey length per species taken from existing literature (15 species) and new data (*Larinioides sclopetarius* and *Argiope keyserlingi*). Pooling the data from all species, the results revealed no significant relationship. Analysing the data from *L. sclopetarius* and *A. keyserlingi* separately, no overall significant relationship was found. However, the analyses of the separate observation days showed that mesh height correlated significantly with prey length on one of the five observation days for *A. keyserlingi*, but not for *L. sclopetarius*. Consequently, the spacing of the sticky spiral in the orb-web can have a significant effect on the length of the captured prey under certain circumstances, which are discussed in the present paper.

INTRODUCTION

Variation in the design of webs constructed by orb-web spiders has been suggested to influence directly the length, kind, and number of prey entangled (Miyashita & Shinkai, 1995). For instance, increasing the web area will reflect in a higher prey capture rate (Chacón & Eberhard, 1980; Herberstein & Elgar, 1994); a greater number of web radii enable the web to absorb more kinetic energy and thus retain heavier and faster flying prey (Craig, 1987; Eberhard, 1990); the "ladder webs" with a vertical extension of the orb constructed by *Kryptaranea atrihastula* (Araneae: Araneidae) are thought to specifically target moths and butterflies (Eberhard, 1980; Forster & Forster, 1985).

However, the role of the mesh height in prey capture is still unresolved. Mesh height refers to the average distance between the capture spirals and, usually, is termed "mesh size". Nevertheless, it is thought that "mesh height" is a more precise description. A relationship between mesh height and prey length has been reported for field populations by Murakami (1983) and Uetz et al. (1978). They argue that a lower mesh height will target prey items with a smaller body length that otherwise may fly through a web with a larger mesh height (see also Risch, 1977). In contrast, under controlled laboratory conditions, using artificial webs, no correlation between prey length and mesh height was found (Nentwig, 1983). This is supported further by a number of field studies (e.g., McReynolds & Polis, 1987; Herberstein & Elgar, 1994). Additionally, mesh height may be a consequence of anatomical constraints rather than being part of a foraging strategy. Vollrath (1987, 1992) argued that mesh height is a result of the length of the leg used to fix the spiral thread onto the radials and that it may also be influenced by abiotic factors such as temperature, humidity or wind (Vollrath et al., 1997). Furthermore, web building behaviour and, consequently, web architecture may also be constrained by phylogenetic factors (Coddington, 1986).

Recently, Sandoval (1994) reported on the extraordinary plasticity in the web design of *Parawixia bistriata* (Araneae: Araneidae). The spider constructed either small sized webs with a lower mesh height which mostly entangled small dipterans, or large webs with a greater mesh height capturing large flying termites only abundant during swarms. The report on this interesting phenomenon reignited the long-standing controversy about the effect of mesh height on prey length in orb-web spiders.

In the present paper, a contribution to this discussion is made by analysing data on mesh height and prey length. If the length of prey is related to mesh height, species constructing webs with a greater mesh height should capture longer prey in comparison with species constructing webs with a lower mesh height. This would result in a significant positive correlation between these two variables. This hypothesis was tested by referring to existing literature on various species and synthesising their measures of mesh height and prey length. While numerous papers described only one of the two variables for a number of orb-web spiders (e.g., Nyffeler et al., 1987; Nyffeler & Benz, 1989; Vollrath, 1992; Tso, 1996), only those which sampled both were analysed (Table 1). In the case of Sandoval's study (1994), the two different web types (small and large) were treated separately.

Additionally, our data included measurements on the mesh height and the prey length for *Larinioides sclopetarius* Clerck (Araneae: Araneidae) and *Argiope keyserlingi* Karsch (Araneae: Araneidae). Most data regarding the web and the prey of orb-web spiders are represented as mean values. Consequently, the mean mesh height and the mean prey length were calculated for our two species and added to the data taken from the literature.

MATERIAL AND METHODS

Data on 50 juvenile nocturnal *L. sclopetarius* were sampled on 5 consecutive nights in July 1996 in Vienna, Austria. The spiders constructed their webs adjacent to artificial lights along the handrails of a footbridge across the Danubian Channel. These lights attracted insects that were captured in the webs (Heiling, pers. obs.). Data on 32 adult diurnal *A. keyserlingi* were sampled on 5 consecutive days in January 1997 in Sydney, Australia and they constructed their webs in the shrub vegetation of a recreational park. The mesh height was calculated from parameters obtained in the field using a formula (Herberstein, unpubl.). Freshly finished webs of *L. sclopetarius* were collected after being exposed for 1 h and fixed in alcohol (76%). In the laboratory, the silk material was dissolved in sodiumhypochloride (1%) and the length of the prey items was measured under a binocular microscope. In contrast, the prey length of *A. keyserlingi* was measured in the field using callipers.

RESULTS

The data set on a total of 17 spider species was analysed using a Pearson correlation test to reveal the nature of the relationship between the average mesh height and average length of entangled prey (Table 1). The results revealed no significant association (R_p = 0.18, n = 19, p > 0.05; Table 1). This indicates that the spacing of the spirals is not necessarily reflected by the length of the captured prey. However, the present analysis between different species did not allow any conclusion regarding individuals within a species. Murakami (1983) found that individuals of *Argiope amoena* (Araneae: Araneidae) that constructed webs with a greater mesh height captured longer prey. Consequently, the sampled prey length and the corresponding mesh height for *L. sclopetarius* and *A. keyserlingi* were correlated using Pearson (R_p) and Spearman rank (R_s) correlations, respectively. In order to avoid pseudoreplication, the mean prey length was used if more than one prey item was found in a particular web, as well as the mean mesh height if a specific individual was sampled more than once.

TABLE 1. Mean mesh height (mm) and mean length of prey (mm) entangled in the webs of 17 orb-web spider species and the methods used to collect the prey. [1] – all prey items found in the webs are considered; [2] – only the wrapped prey items are considered; [3] – no details given.

Species	Mesh height	Prey length	Source
Argiope argentata	3.7	2.8	[1]Nentwig, 1985
Cyclosa conica	2.5	2	[3]Nentwig, 1983
Eriophora fuliginea	5.6	2.2	[1]Nentwig, 1985
Meta reticulata	3.9	2	[3]Nentwig, 1983
Nephila clavipes	2.6	2.1	[1]Nentwig, 1985
Parawixia bistriata I	1.4	2	[1]Sandoval, 1994
Parawixia bistriata II	4.5	8.3	[1]Sandoval, 1994
Argiope aurantia	4.6	16.3	[2]Uetz et al., 1978
Argiope trifasciata	2.7	10.2	[2]Uetz et al., 1978
Leucauge venusta	1.9	3	[2]Uetz et al., 1978
Mangora placida	1.1	4	[2]Uetz et al., 1978
Micrathena gracilis	1.4	7	[2]Uetz et al., 1978
Araneus diadematus	5.6	2.9	[1]Walker, 1992
Zygiella x-notata	3.4	2.4	[1]Walker, 1992
Eriophora transmarina	7.5	5.7	[2]Herberstein & Elgar, 1994
Nephila plumipes	2	5.4	[2]Herberstein & Elgar, 1994
Argiope keyserlingi	3.5	5.1	[2]This study
Larinioides sclopetarius	2	2.5	[1]This study

The mesh height in the webs of *L. sclopetarius* and *A. keyserlingi* was not related to the prey length entangled ($R_p = 0.13$, $n = 50$, $p > 0.05$ and $R_p = 0.21$, $n = 32$, $p > 0.05$; respectively), pooling the data from all observation days. However, when analysing the data day by day, a significant relationship was revealed on one of the five sampled days for *A. keyserlingi* ($R_s = 0.58$, $n = 24$, $p < 0.01$) but never for *L. sclopetarius*. This phenomenon may be an artefact of sample size as the sample size on this day was greatest ($n = 24$) compared to the other days ($n = 6–11$) and a larger sample size on those days may have also revealed a significant result for *A. keyserlingi*.

DISCUSSION

A possible reason why a significant relationship is found in one species, but not the other, may be the different sampling methods used. For example, Nentwig (1985) pooled data collected over an entire year, whereas Walker (1992) pooled data collected over a period of 6 weeks. In contrast, Sandoval (1994) who found that webs with a greater mesh height captured longer prey, sampled only over several days. Pooling data over longer observation periods may, thus, result in the loss of important information, such as significant associations on certain days only. Ideally, large data sets need to be analysed on a day by day basis.

Similarly, in some studies, all items entangled in the web were considered as prey (Nentwig, 1985; Sandoval, 1994; Walker, 1992; and *L. sclopetarius* in this study) while other studies considered only those that were wrapped by the spider (Uetz et al., 1978; Herberstein & Elgar, 1994; *A. keyserlingi* in this study). Orb-web spiders have been shown to ignore small and unprofitable prey (Herberstein et al., in press) and as a consequence, considering only the wrapped prey may overestimate prey length. In subsequent analyses the data from those studies with comparable prey collection methods were correlated but, again, the results revealed no relationship between mesh height and prey length in studies that considered all prey in the web ($R_p = 0.3$, $n = 8$, $p > 0.05$) or only those that were wrapped ($R_p = 0.29$, $n = 8$, $p > 0.05$). The data from Nentwig (1983) were not used as no details of the methods were given.

Furthermore, the range of prey length available to the spiders may also play an important role. The preferred web site of *L. sclopetarius* is adjacent to water (Heiling & Herberstein, in press), where the spiders almost exclusively capture small dipterans (range: 1.2–6.8 mm, n = 426; two prey items with a prey length of 11.3 mm were excluded), providing little variation in prey length. Likewise, in a population near Zürich (Switzerland), small dipterans also composed 94% of the total prey of *L. sclopetarius* (Nyffeler, pers. commun.). In contrast, the prey spectrum of *A. keyserlingi* has a higher diversity and thus greater prey length variation (range: 2.0–22.0 mm, n = 110). Obviously, differences in mesh height may only influence prey length if a diverse potential prey spectrum is abundant. The contradictory results found in the literature may, thus, also reflect the presence or absence of sufficient variation in prey length. Variation in mesh height may, equally, be influenced by the proportion of juveniles and adults in a population. For instance, mesh height in *L. sclopetarius* is related to the body size of juvenile spiders, but not to that of adults (Heiling & Herberstein, in press).

Whereas the present analyses of published data do not support the idea that the mesh height generally corresponds to the prey length, it is concluded that it may have a significant effect on the length of the captured prey under some circumstances, depending on factors such as observation methods, diversity of the available prey, and variation in mesh height.

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