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Web inclination alters foraging success of a nocturnal predator

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ABSTRACT

In spider species, web inclination (vertical and horizontal webs) plays an important role in foraging success. However, these effects are poorly understood especially in such spiders that build both vertical and horizontal orb-webs. Recent studies have shown that spider species with horizontal orb-webs are specialized in preying aquatic insects emerging from the water. Females of a nocturnal orb-weaving spider, *Larinioides cornutus,* are able to build both vertical and horizontal orb-webs. Contrary to expectations, spiders which built horizontal orb-webs made higher expenditures in the form of sticky spirals and captured less prey in comparison with females in vertical webs. Moreover, horizontal webs were not closely related to water, as might have been expected given their potential function of catching aquatic insects, despite the probability of successful foraging was generally higher in webs placed closely to water stream. On the other hand, the probability of a web being destroyed was higher in vertical orb-webs, which may indicate that horizontal webs may be a compromise between more successful, but less lasting capture traps that would benefit from exposition during windless days and vice versa.

KEY WORDS: *Larinioides cornutus* - Foraging behaviour - Spider - Web inclination.

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INTRODUCTION

Orb-weaving spiders are traditionally referred to as sit-and-wait predators that typically invest only a little of their energy after the orb-web has been constructed (Uetz, 1992). Therefore, before building a web the spider must make the most important decision which will affect its future foraging success. There are several ways in which spiders can improve this target. First, they may choose web sites where there is abundance of food (Olive, 1980, 1982; Nakata & Ushimaru, 1999; Heiling, 1999) and/or leave a recent site if the webs are frequently damaged (Chmiel *et al*., 2000). Second, they may also adjust the design of their webs to increase the rate they capture prey (Sherman, 1994; Tso, 1999; Seah & Li, 2002); for example, if the web is larger, more prey will be captured (Chacón & Eberhard, 1980; Higgins & Buskirk, 1992; Herberstein & Elgar, 1994; Prokop & Gryglákovä, 2005). Mesh size, which affects visibility of the orb-web (Craig & Freeman, 1991), can also be altered in accordance with the presence of specific types of prey (Sandoval, 1994; Schneider & Vollrath, 1998).

Web inclination also plays a significant role in spider's foraging success. In the case of orb-weaving spiders, it enhances visibility of the web (Nyffeler & Breene, 1991); for example, prey may have difficulty in detecting horizontal webs from below because the web is camouflaged into the background (reviewed by Eberhard, 1990). Horizontal webs are therefore expected to have greater advantages for orb-web spiders that are distributed along water streams, as they would target aquatic insects emerging from the water (Buskirk, 1975; Chacón & Eberhard, 1980; Henschel *et al*., 2001).

Recently, Kato *et al*. (2003) showed the significant impact of aquatic insect density on the distribution of horizontal orb-weaving spiders (from the family Tetragnathidae), that are specialized in preying insects emerging from the water. However, some araneids (Araneidae) that are typically considered to be vertical orb-weavers (cf. Kato *et al*., 2003) build both horizontal and vertical orb-webs. The origin of this web building dimorphism is unclear. In addition, there is no positive effect of horizontal webs on the interception of prey (Chacón & Eberhard, 1980) or of prey being retained in them (Eberhard, 1989). In the present study, I examine: 1) the effects of proximity to water on web design and how this affects prey capture, and 2) the effect of horizontal and vertical orb-webs on the foraging success of *Larinioides cornutus* (Clerck, 1757) adult females that inhabit vegetation near water streams (Kajak, 1965; Sherman, 1994).

MATERIALS AND METHODS

The study was conducted from June to August 2003 near the city of Senec (48°21' N, 17°31' E), western Slovakia. The study area was beside a water stream and was mostly covered by stinging nettles (*Urtica dioica*) and stem (*Phragmites australis*). On observational days, about 15 orb-webs with the adult *L. cornutus* females in 20-30 m × 1.5 m transects were located and marked with white ribbon on the nearest plant. Then vertical diameter, mesh height (nearest distance between two spirals), web height (from the ground to the web hub), height of the plants to which the orb-web was attached, and distance of the web from the water were measured. Transects were located randomly on both sides of the water stream. To minimize observation of the same spider, each transect was used only once. The success of prey capture was estimated by surveying each spider's web every 30 minutes from 5:00 a.m. until 11:00 a.m. All prey captured in the orb-webs were measured using digital calliper and identified to the level of insect order. To avoid disturbance of observed spiders, prey was measured directly in the orb-webs. Most of the insects captured in orb-webs were mosquitoes (Diptera Chironomidae) emerging from the water. They were also the most frequent prey of observed spiders (see below). I therefore used them as a model of the aquatic insect that would be one of the most important prey for spiders occupying the water surface, such as *L. cornutus*. Body mass of prey was estimated from body length, using the regression equation of Rogers *et al.* (1976):

$$\text{Mass} = 0.0305 \times \text{length}^{2.62}.$$

This formula was recently also used by Nakata *et al.* (2003) in a similar situation. All webs with 0-10° deviation of web plane from vertical were considered vertical webs. Webs with approximate deviation 80-90° of web plane from vertical were considered horizontal webs.

In total, 133 orb-webs were observed, but in seven cases the spider ate their webs before the end of the observations. In another 21 cases, two thirds of the orb-web was destroyed due to unknown reasons (probably weather conditions). For the comparison of foraging success, I therefore included only data from the remaining 105 spider webs analysed. Only sunny (±30 °C), non–consecutive days were selected for observations. All statistical tests are two–tailed and data are presented as mean ± SE.

RESULTS

Effects of environmental variables

Average values of measured variables are shown in Table I. The weight of prey was not normally distributed (Kolmogorov-Smirnov test); ln(x+1) transformed data of body mass was therefore used as the dependent variable in multiple regression. Vertical diameter of the orb-web, mesh height, web height and distance from the water were included as independent variables. A strong correlation was observed between web height and length of supporting plants ($r = 0.91$, $P < 0.0001$, $n = 105$), and so only web height was used for subsequent analyses. All variables entered the multiple regression model ($R^2 = 0.11$, $F_{4,100} = 3.17$, $P = 0.02$), thus web height and distance from the water were considered the best predictors of spiders' foraging success (Table II, Fig. 1).

The effect of web inclination.

Although there were no differences in the mean number of prey per web detected by comparing horizontal and vertical orb-webs, it was discovered that length and biomass of captured prey did significantly differ between both types of orb-webs ((ln) vertical vs horizontal: 2.28 ± 0.22 vs 1.22 ± 0.25, $n_1 = 88$, $n_2 = 17$, t-test with equal variances not assumed, $t_{44.454} = 3.16$, $P = 0.003$). Contrary to expectation, the proportion of flies (Diptera) was significantly higher in vertical (458 of 610, 75.08%) rather than horizontal (42 of 95, 44.21%) orb-webs ($\chi^2 = 37.99$, df = 1, $P < 0.0001$, chi-square test). The probability of capturing flies in the web was negatively related with the distance from the water ($r = -0.24$, $P = 0.02$, $n = 94$; 11 empty webs excluded). After excluding horizontal webs from the analysis, the correlation became even closer ($r = -0.28$, $P = 0.01$, $n = 80$).

I analysed differences in all measured variables between horizontal and vertical orb-webs (Table I) and, surprisingly, horizontal webs had higher vertical diameter than did vertical orb-webs. Interestingly, vertical webs contained fewer spirals than horizontal ones. Other variables remained non significant.

Horizontal webs were less successful in comparison with vertical ones (they captured less biomass during the observation period), although the probability of their being destroyed was lower, because all webs that were excluded from the analyses because of destruction were vertical ones (21 out of 109 vertical webs vs 0 out of 17 horizontal webs; $\chi^2 = 3.93$, $P = 0.047$).

TABLE I - *Comparison of vertical and horizontal orb-web measurements (t-tests).*

Measured variable	Vertical webs (n = 88)			Horizontal webs (n = 17)			P
	Mean	SE	Range	Mean	SE	Range	
No. of spirals	55.40	1.48	17-84	67.06	3.22	47-92	<0.01
Vertical diameter (cm)	32.46	0.87	14.8-53.7	41.01	2.24	28.2-59.3	<0.001
Mesh height (cm)	0.52	0.01	0.29-0.81	0.53	0.02	0.41-0.76	0.71
Web height (cm)	102.16	3.16	30-200	115.71	6.48	70-162	0.08
Mean length of supporting plants (cm)	118.76	3.08	40-215	129.74	6.85	85-189	0.15
Distance from the water (cm)	39.31	5.22	-80-130	44.52	6.86	-5-80	0.54
No. of captured prey	7.18	0.90	0-39	5.88	1.17	0-18	0.38
Average length of prey (cm)	0.76	0.11	0.1-4	0.31	0.04	0.1-0.7	<0.001

TABLE II - *Effects of several independent variables on foraging success of* L. cornutus *(results from the multiple regression model).*

Factor	Beta	t	P
Web height	-0.24	-2.47	0.02
Vertical diameter	0.04	0.37	0.71
Distance from the water	-0.22	-2.21	0.03
Mesh height	-0.04	-0.39	0.70

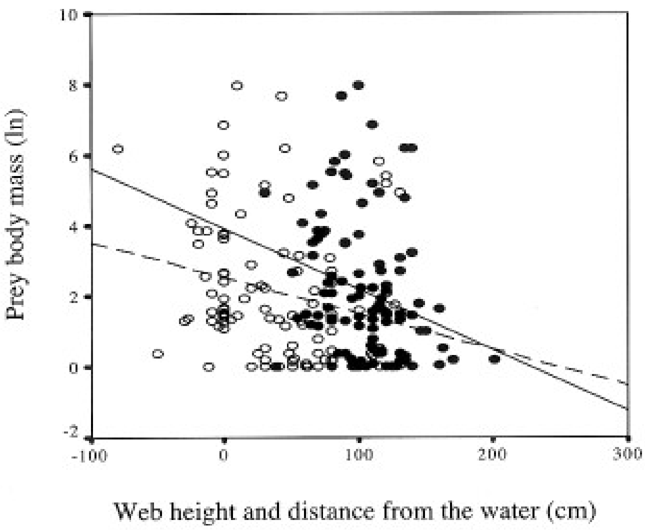

Fig. 1 - Relationships between spiders' foraging success and web height (● solid line) and distance from the water (○ broken line).

DISCUSSION

This study showed a significant effect of water streams for female *L. cornutus* foraging success, while the significance of building vertical and/or horizontal orb-webs still remains puzzling. Although several reports about the effect of prey abundance on spider movement exist, the effect of closeness to water streams and/or their potential effect on intraspecific competition has not been directly examined. Heiling & Herberstein (1999b) showed that the body condition of immature nocturnal spiders *L. sclopetarius* was significantly affected by the presence of artificial light, which attracts insects and spiders occupying the habitat. This kind of site leads to higher foraging success in comparison with spiders from dark web sites. Heiling (1999) suggested that nocturnal orb-web spiders such as *Larinioides* may have originally used reflected moonlight as an indicator for high insect densities, and thus as a cue to improve their foraging success. She also showed that both inexperienced and experienced spiders preferred artificially lit sites which may indicate that a spider's active search for lit patches may be genetically determined. Both *L. cornutus* and *L. sclopetarius* occupy similar habitats (P. Prokop, personal observations); they both have nocturnal activity and are phylogenetically related, similar patterns to those found by Heiling (1999) for *L. sclopetarius* could be predicted for *L. cornutus*. Thus, competition for suitable microhabitats beside water may exist.

One might predict that the spiders living close to the water will benefit from the insects constrained in the water. This was confirmed by the prevalence of flies in the diet of observed spiders. Surprisingly, although horizontal orb-webs are considered to be specialized traps for insects emerging from the water (Kato *et al.*, 2003), no relation between the distance to the water or between proportion of flies and horizontal webs was shown. Moreover, investments in sticky spirals in horizontal webs were larger in comparison with those in vertical ones. This fact can appear surprising, because large webs have been considered to capture more prey (Chacón & Eberhard, 1980; Higgins & Buskirk, 1992; Herberstein & Elgar, 1994, Prokop & Gryglákovâ, 2005), but horizontal webs in this study were less successful in capturing prey (see also Chacón & Eberhard, 1980 for comparison). No relation between web diameter, mesh height and prey interception can be explained by the location of the site near the water stream. However, this gives rise to the question why spiders invest in costly orb-webs. There is strong positive correlation between vertical diameter of the web and the number of spirals per web. Although webs with higher number of sticky spirals are widely meshed, I showed that web diameter was greater in horizontal orb-webs, but mesh height did not significantly differ. This means that costs were associated with longer capture threads and probably with web building behaviour.

There are several explanations why horizontal webs are constructed (see also Eberhard, 1989, 1990). First, abiotic factors, such as wind and rain can affect web inclination. In this case, one would expect horizontal webs to be damaged less by wind than by rain. Second, horizontal orb-webs need less expenditure for the building of the web. Horizontally oriented webs are mostly symmetrical (Vollrath, 1992) and expenditures for the vertical building (which are usually asymmetrical) of the orb-webs are comparatively different between the upper and lower web region (e.g. Heiling & Herberstein, 1999a). Investment in web building (in terms of energy spent during web construction) would be generally different. Third, microhabitat properties, i.e. the density and height of plants available for web attachment. In the presence of few plants or less dense vegetation, the probability of building horizontal webs would be higher. Fourth, Heiling & Herberstein (1999a) found that web building behaviour is affected by a spider's experience. Although their study was related to changes in web design, the potential influence of a spider's experience on web inclination should not be ruled out.

The first explanation can be indirectly supported by the present data, because the probability of a web being destroyed was different in both types of orb-webs. Moreover, the types of web damage indicate that vertical webs were largely destroyed by the wind (cf. Craig, 1989), although only days with minimal wind strength were selected for observations. It is probable that spiders with horizontal webs will benefit from foraging prey later in the day, when their abundance along water streams increases (see Buskirk, 1975). The second explanation cannot be confirmed without experimental evidence, while the last two explanations seem less probable, because 1) found no differences in web height or attached plants between horizontal and vertical webs, 2) that density of the vegetation near the water was homogeneous and very dense, and 3) only adult and therefore experienced females were used for observations.

This study raised several questions, which will need further research regarding foraging success and the building of the horizontal orb-webs by spiders.

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