

Factors influencing the size of the orb web in *Araneus diadematus*

Samuel ZSCHOKKE

Department of Zoology, South Parks Road, Oxford, OX1 3PS, England and Zoologisches Institut, Rheinsprung 9, CH-4051 Basel, Switzerland.

Current address: Institut für Natur-, Landschafts- und Umweltschutz, Universität Basel, St. Johanns-Vorstadt 10, CH-4056 Basel, Switzerland.

Key words: spider, behaviour, orb web, investment, web size, constraint.

ABSTRACT

The size of the web built by *Araneus diadematus* is influenced by several factors. The single most important factor is - of course - the size of the spider, but other factors also play a role. One of these factors is the supply of silk in the glands of the spider. In this study, the influence of the supply of silk (deduced from the time since the spider had built its previous web) on the size of the web is quantitatively analysed. It was found that the time since the spider had built the previous web significantly influenced the size of the current web, but only if the current web was built within 20 hours after the previous one.

INTRODUCTION

Spiders build webs of varying sizes. The decision by the spider to build a web of a certain size is influenced by several factors (Tab. 1). Of these factors, the most important ones are certainly the species and the size of the spider. In an experiment designed to show the influence of silk supply on web size, Eberhard (1988) has shown that webs built during the day - after the web the spider had built during the night had been destroyed by the experimenter - were smaller than the ones built in the night. He concluded that the spiders were constrained by their silk supply when they built the second web. Similar observations have been made by Vollrath (1992).

In our laboratory, I observed the construction of several webs built in a series by the same spider. I could show that the size of the web correlated with the time since this spider had built the previous web, as long as this time was less than 20 hours. No correlation could be found if the time since building the previous web was longer than 20 hours.

MATERIAL AND METHODS

For this study, I used 11 juvenile *Araneus diadematus* of a similar size, caught in the wild. The construction of a series of webs by each spider was recorded using the methods described in (Zschokke 1994). After each web construction, the spider was fed with 1 fruit-fly *Drosophila* sp. and the web was sprinkled with water. The spider was then removed from the web and the web was thoroughly destroyed and the frame was wiped off to remove all remains of the old web. The spider was not allowed to ingest the old web. The spider was then re-released onto the frame to build another web.

From the recorded data I extracted the time the web was finished and the distance the spider had covered to build the capture spiral as a measure for the amount of sticky silk used to build the web. I focused on measuring this distance over measuring the web-area because it better reflects the investment of the spider. With the same investment a spider can either build a large, widely spaced web or a smaller, finely spaced one.

The distance used to build the capture spiral was analysed using an ANCOVA with the spider as a factor and the time since completion (termed Δt) of the previous web as covariant. Two separate comparisons were made, one with webs where the time since the previous web was less than 20 hours ($\Delta t < 20$, $n = 35$) and one where the time since completion of the previous web was more than 20 hours ($\Delta t > 20$, $n = 27$). Since there were no differences between spiders for webs built less than 20 hours after the previous one, a regression was calculated between Δt and the distance the spider had walked to build the capture spiral.

RESULTS

The ANCOVA (Tab. 2) for the webs built less than 20 hours later than the previous web indicated a significant ($p = 0.0001$) influence of the time since the last web and the distance the spider had walked to build the capture spiral. There was, surprisingly, no effect for spider ($p = 0.79$) and no interaction between the two factors ($p = 0.53$). This allowed me to pool all spiders and calculate the regression of the distance walked to build the capture spiral and the time elapsed since completing the previous web (Fig. 1). This gave again a significant result, with a regression line of $y = 4.15 + 0.24x$ ($r^2 = 0.64$, $p < 0.0001$, $n = 35$).

The ANCOVA for the webs built more than 20 hours after the previous web showed, that the elapsed time had no influence ($p = 0.75$) on the size of the web. There was also no significant effect for spider ($p = 0.16$) and no interaction between the two factors ($p = 0.23$).

Additional similar analysis of web area, number of spiral loops, number of radii and mesh size, gave similar results for web area and number of spiral loops. There was however no significant influence of Δt on number of radii and mesh size (Tab. 3).

Tab. 1. Known factors influencing the size of a web.

factor	effect
size of the spider	larger spiders build larger webs (e.g. Peters 1939; Witt & Baum 1960; Witt <i>et al.</i> 1972; Benforado & Kistler 1973; Risch 1977; Eberhard 1988; Higgins & Buskirk 1992).
weight of spider	heavier spiders of same size build larger webs (Eberhard 1988). Spiders with artificial weight increase (lead) build more widely meshed webs of a similar size (Mayer 1952; Witt & Baum 1960; Christiansen <i>et al.</i> 1962)
prey availability	lower prey availability leads to larger webs (Higgins & Buskirk 1992; Sherman 1994), but see (Witt 1963a).
weather conditions	increase in barometric pressure, increase in hours of sunshine and decrease in precipitation lead to larger webs (Ammitzbo 1988).
available space	limited available space leads to smaller webs (Szlep 1958).
egg production	egg production leads to smaller webs (Sherman 1994).
web built from scratch	webs built from scratch are smaller than webs built to replace existing webs (Zschokke 1994).
supply of silk in glands	see text (Eberhard 1988; Vollrath 1992).

Tab. 2. One factor ANCOVA of the distance the spider walked to build the capture spiral. The spider was used as factor and the time since building the previous web (Δt) as covariate. The data was separated into two groups. One with the webs where the time since building the previous web was less than 20 hours ($\Delta t < 20$, $n = 35$, shown on the left) and the other group with $\Delta t > 20$ ($n = 27$, shown on the right).

Source	$\Delta t < 20$				$\Delta t > 20$			
	df	MS	F	p	df	MS	F	p
spider	5	0.31	0.47	0.792	6	1.74	1.90	0.161
Δt	1	22.29	34.01	0.0001	1	0.10	0.11	0.749
spider * Δt	5	0.56	0.85	0.528	6	1.46	1.59	0.232
Residual	23	0.66			12	0.92		

Tab. 3. Probabilities calculated in one Factor ANOVA's of distance covered to build capture spiral, web area, number of spiral loops, number of radii and mesh size to be influenced by spider, time elapsed since previous web construction and interaction between the two. The data was separated into two groups. One with the webs where the time since building the previous web was less than 20 hours ($\Delta t < 20$, $n = 35$, shown on the left) and the other group with $\Delta t > 20$ ($n = 27$, shown on the right).

measured parameter	$\Delta t < 20$ (n = 35)			$\Delta t > 20$ (n = 27)		
	spider	Δt	spider* Δt	spider	Δt	spider* Δt
distance covered to build capture spiral	0.792	0.0001	0.528	0.161	0.749	0.232
web area	0.291	0.0001	0.531	0.147	0.641	0.142
# spiral loops	0.536	0.0001	0.636	0.058	0.513	0.196
# radii	0.061	0.051	0.555	0.352	0.607	0.984
mesh size	0.002	0.275	0.689	0.230	0.943	0.002

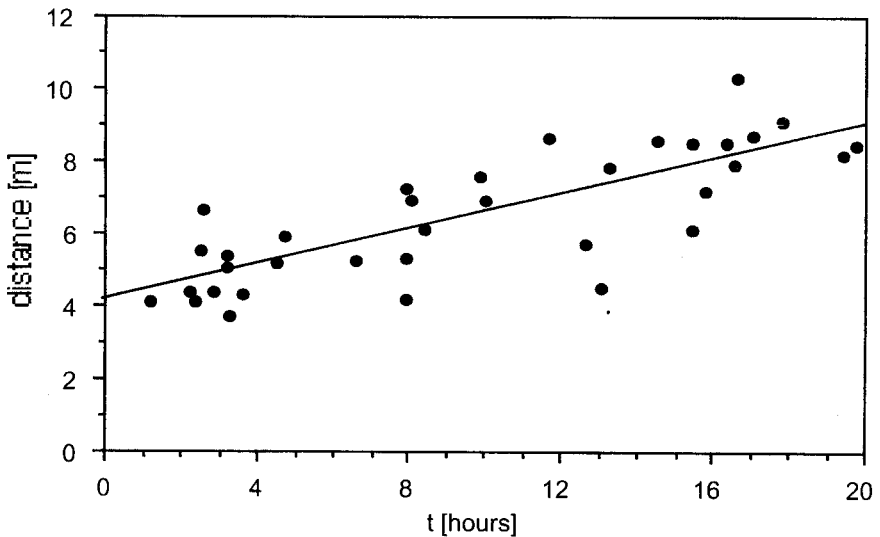


Fig. 1. Regression between the time since the spider had built a previous web (Δt) and investment into the web expressed as the distance the spider had walked to build the capture spiral ($y = 4.16 + 0.24x$, $r^2 = 0.637$, $p < 0.0001$, $n = 35$). Only webs where the time since the previous web (Δt) was less than 20 hours were used in this analysis.

DISCUSSION

My results are in agreement with the hypothesis that the spiders synthesise silk to fill their glands and adjust the size of the web to the amount of silk stored in their glands. The difference between webs built less or more than 20 hours after the previous web suggests that the silk glands are full up after 20 hours after completing a web. This corresponds well to the usual 24-hour cycle in which *Araneus diadematus* renews its web (Breed *et al.* 1964; Carico 1986).

The fact that the regression does not go through the origin furthermore suggests that the spider does not deplete their glands, at least not when building a web from scratch as in my experiments. It is possible that the spider leaves a 'strategic' reserve in their glands when building a web from scratch, since the new site may be unproductive (Riechert & Gillespie 1986). This may explain the contradictory observations by Witt (1963b) who claimed that not much material was left in the glands directly after orbs were built.

We have thus shown quantitatively that the spiders are able to adjust the investment into their web according to the supplies of silk left in their glands.

Acknowledgements

This study has been carried out as a partial fulfilment of Samuel Zschokke's PhD Thesis and has been financed by a grant of the Swiss National Science Foundation to Fritz Vollrath. I am grateful to Fritz Vollrath for his advice and help and to Soren Toft for sending me valuable information on the influence of the weather on web construction.

REFERENCES

- Ammitzbo A. 1988. Foraging hos *Araneus quadratus* Clerck (Foraging in *A. q.*). Masters thesis, University of Aarhus.
- Benforado J. & Kistler K. H. 1973. Growth of the orb weaver, *Araneus diadematus*, and correlation with web measurements. *Psyche*, **80**: 90-100.
- Breed A. L., Levine V. D., Peakall D. B. & Witt P. N. 1964. The fate of the intact orb web of the spider *Araneus diadematus* Cl. *Behaviour*, **23**: 43-60.
- Carico J. E. 1986. Web Removal Patterns in Orb-Weaving Spiders. In: Shear W. A. (ed.), *Spiders: Webs, Behavior and Evolution*. Stanford University Press, Stanford, pp. 306-318.
- Christiansen A., Baum R. & Witt P. N. 1962. Changes in spider webs brought about by Mescaline, Psilocybin and an increase in body weight. *J. Pharmacol.*, **136**: 31-37.
- Eberhard W. G. 1988. Behavioral flexibility in orb web construction: Effects of supplies in different silk glands and spider size and weight. *J. Arachnol.*, **16**: 295-302.

- Higgins L. E. & Buskirk R. E. 1992. A trap-building predator exhibits different tactics for different aspects of foraging behaviour. *Anim. Behav.*, **44**: 485-499.
- Mayer G. 1952. Untersuchungen über die Herstellung und Struktur des Radnetzes von *Aranea diadema* und *Zilla x-notata* mit besonderer Berücksichtigung des Unterschiedes von Jugend- und Altersnetzen. *Z. Tierpsychol.*, **9**: 337-362.
- Peters H. M. 1939. Über das Kreuzspinnennetz und seine Probl. *Naturwiss.*, **27**: 777-786.
- Riechert S. E. & Gillespie R. G. 1986. Habitat Choice and Utilization in Web-Building Spiders. In: Shear W. A. (ed.), *Spiders: Webs, Behavior and Evolution*. Stanford University Press, Stanford, pp. 23-49.
- Risch P. 1977. Quantitative analysis of orb web patterns in four species of spiders. *Behav. Genet.*, **7**: 199-238.
- Sherman P. M. 1994. The orb-web: an energetic and behavioural estimator of a spider's dynamic foraging and reproductive strategies. *Anim. Behav.*, **48**: 19-34.
- Szlep R. 1958. Influence of External Factors on Some Structural Properties of the Garden Spider (*Aranea diademata*) Web. *Fol. Biol.*, **6**: 287-299.
- Vollrath F. 1992. Analysis and interpretation of orb spider exploration and web-building behavior. *Adv. Stud. Behav.*, **21**: 147-199.
- Witt P. N. 1963a. Environment in Relation to Behavior of Spiders. *Arch. Envir. Health*, **7**: 4-12.
- Witt P. N. 1963b. Interrelationships between web-building behavior and amount of thread material in the spider *Araneus diadematus* Cl. XVI Int. Congr. Zool., Washington, D.C., p. 7.
- Witt P. N. & Baum R. 1960. Changes in orb webs of spiders during growth (*Araneus diadematus* Clerck and *Neoscona vertebrata* McCook). *Behaviour*, **16**: 309-318.
- Witt P. N., Rawlings J. O. & Reed C. F. 1972. Ontogeny of web building behaviour in two orb weaving spiders. *Amer. Zool.*, **12**: 445-454.
- Zschokke S. 1994. Web construction behaviour of the orb weaving spider *Araneus diadematus* Cl. PhD Thesis, Universität Basel, 177 pp.