

The effect of starvation on web geometry in an orb-weaving spider

Fritz Vollrath^{1,2} and Ferenc Samu^{1,3}

¹Department of Zoology,
South Parks Road,
Oxford, OX1 3PS

²Department of Zoology,
Universitet B135,
DK 8000 Aarhus C, Denmark*

³Plant Protection Institute,
PO Box 102,
H 1525 Budapest, Hungary

Summary

Starving juvenile *Araneus diadematus* (Araneae, Araneidae) cross spiders led to an increase in the frequency of web-building activity as well as to a higher variability in web geometry (mesh and capture area). An increase in food led to a decrease in web-building frequency as well as some web fine-tuning (by increasing capture area). Our laboratory data obtained under controlled conditions support the interpretation of field studies by others which suggested that spiders may be capable of responding to changes in prey availability by adjusting the architecture of their webs.

Introduction

Web-building spiders are sit-and-wait predators with high costs of moving from one web site to another. These costs are due partly to high predation risks when travelling (Vollrath, 1985), partly to a lack of information about the economic value of the present web site as opposed to the marginal value of the environment (Janetos, 1986) and partly to the risks associated with finding a better site mostly by trial and error (Enders, 1977). Notwithstanding these high costs, web spiders do modify their residency time at a given web-site according to local prey density by staying longer when food is abundant and moving more or less promptly when it is not (Janetos, 1982, 1986; Olive, 1982; Vollrath & Houston, 1986). However, apart from responding to prey density by adjusting site tenacity, web spiders could also respond by staying in the same place but adjusting their prey capture strategy and thus reducing metabolic costs (Vollrath, 1987). This might be achieved by altering web-building behaviour such as rebuilding frequency and/or construction behaviour responsible for web architecture.

The question whether spiders can and do adjust web-building behaviour was first considered by Disjonval (1797) who, confined to the Bastille for a considerable sojourn at the king's pleasure, observed the spiders building between the bars of his window. He observed that web-building frequency and web parameters were affected by the weather as well as by prey. The issue was taken up again by Witt *et al.* (1968) who found that *Zygiella x-notata* (Clerck) cease web-building

for a number of days when well-fed. Witt and collaborators also studied the effect of starvation on the amount of silk used for a web, and on the size of the web. They found: (i) that the total amount of silk available declined a few days after the onset of starvation but (ii) that the area covered by the web began to decrease only after about a week of starvation. These observations led to the conclusion that these spiders compensate for a decrease in prey by maintaining a large web area even if silk protein (because of malnutrition) is becoming a scarce commodity. Subsequent studies have investigated the effects of prey availability in the field and have found significant numerical responses in life history parameters (Spiller, 1992) as well as functional responses in prey capture behaviour (Leborgne *et al.*, 1991; Pasquet *et al.*, 1994). Recently Sherman (1994) addressed the issue of variability of web parameters and found that in the spider *Larinioides cornutus* (Clerck) "hungry spiders invest more effort into foraging, while sated spiders re-allocate energy from continued foraging to egg-production". Sherman's observations encouraged us to report a controlled experiment which bears on this issue.

Material and methods

We studied the web-building frequency and web architecture of the orb-weaver *Araneus diadematus* Clerck in response to different feeding regimes in our laboratory under highly controlled conditions. The animals were raised and kept individually under our standard laboratory conditions (Samu & Vollrath, 1992) in 30 × 30 × 5 cm frames; 16:8 L:D, 25°C, 50% RH, watered daily by spraying. Immature and subadult female spiders of previously identical feeding history were allocated to one of three feeding treatments: (A) starvation, no food at all; (B) control, 1 fruit fly daily (wild type *Drosophila melanogaster*); and (C) satiation, 10 fruit flies daily. Before the trials, spiders in A and B were given 1 fly daily for a week; spiders in treatment C were starved for a week. In each treatment 4 spiders built good webs (i.e. typical orbs) at a frequency sufficiently high for statistical analysis. Webs were photographed, digitised (to an accuracy of 0.05 mm) and analysed by calculating a number of web characteristics (see Samu & Vollrath, 1992). Since many of these parameters are interrelated, only two were chosen to represent the changes in webs: area covered by the sticky spiral (capture area) and the average distance between consecutive spiral turns (mesh size), measured on one radius in the south (lower) part of the vertical webs. These are two robust and independent parameters that greatly influence prey capture (Rhisiart & Vollrath, 1994); they were also used by Witt *et al.* (1968) and Sherman (1994). We analysed the data with a 3rd order polynomial regression.

Results and discussion

Our data showed that well-fed spiders reduced web-building frequency whereas starving spiders increased it (Fig. 1). We, unlike Witt *et al.* for *Zygiella* (1968), found

*Address for correspondence: Prof. Fritz Vollrath, Department of Zoology, Universitetsparken B135, DK 8000 Aarhus C, Denmark.

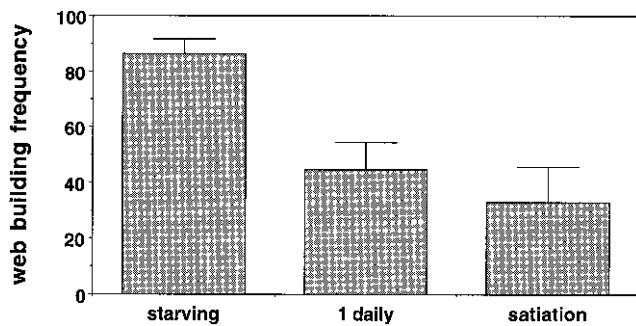


Fig. 1: Web-building frequency of spiders in the three feeding treatments (number of days web built/total number of treatment days (+S.E.)). The treatment starvation (0 flies, $n=4$) lasted 40 days, standard (1 fly daily, $n=6$) lasted 16 days and satiation (10 flies daily, $n=4$) lasted 8 days. The differences between the three treatments were tested with paired t-tests and were significant between the diets starvation and 1 fly ($p=0.052$, $t=3.13$), as well as 10 flies ($p=0.01$, $t=5.19$), but not between 1 and 10 flies ($p=0.53$, $t=0.71$).

that overfed *Araneus* suspend web-building not immediately but after about 8 days; and at that time they were ready to moult and had to stop web-building. Our spiders as opposed to Witt's, however, were all immature as well as a different species, and might have had a feeding strategy different from *Zygiella*. To study the observed changes in web geometry in more detail, we plotted web parameters against time (Fig. 2). In contrast to Sherman's, our spiders had been raised under highly controlled conditions and were studied under these same conditions which differed only in the treatment (diet). Yet we, like Sherman, observed high individual variability in web geometry (Fig. 3) which renders difficult any analysis of the effects of diet. Our spiders were also (i) controlled as to state within an instar (not too close to either preceding or following moult), (ii) were all immatures (not concerned with reproduction, like Sherman's spiders which were adults) and (iii) had been collected as second instars in one small, isolated locality (suggesting genetic similarity). This, in combination with our highly controlled laboratory environment and full security of a spider's identity (supported by the most accurate measuring possible), suggests strongly that the observed variability is not an artefact but real. It seems largely a matter of internal state, maybe fluctuating semi-randomly. From our reasonably large sample of spiders we further analysed only those (75% per treatment) that built webs at least every other day (with the exception of the starvation treatment). Here, too, subsequent webs of individual spiders showed large and inexplicable fluctuations in web parameters obscuring trends that might have occurred during the course of the experiment (Fig. 2).

Spiders on the starvation treatment were followed the longest. Over 5 weeks of complete starvation was insufficient to produce any clear (significant) trends in web area or mesh size, since later webs were in size and geometry comparable to earlier ones, even towards the end of the experiment (with the exception of the last 2–3 days, which statistically were irrelevant). Although aware that "absence of evidence is not evidence of absence" we deduce that spiders in an environment with

declining quality and unable to move away do not adjust (fine-tune) their web-building algorithm. We failed to find changes in web fine-tuning in the treatment where 1 fly was given daily; of our diets this was probably the closest to the natural rate of food intake (Vollrath, 1988). In contrast, the treatment in which 10 flies were given daily had a significant ($r^2=0.663$, $p<0.001$) effect on web geometry, with spiders increasing web area by approximately 100% and slightly (but insignificantly) decreasing mesh size soon after the onset of the treatment. It could be argued that this behaviour would serve to exploit better a fortuitous increase in a resource.

Our results of the "starvation to rich diet" contradict the observations of Witt *et al.* (1968) who found that *Zygiella x-notata* under similar (but obviously not identical) laboratory conditions of a sudden food increase retained the original size of their webs. Sherman's (1994) "normal to rich diet" spiders were adults in the wild which could and did lay eggs, and thus had a reproductive component that our spiders (being juveniles) lacked. Accordingly our experiments could be seen as only providing additional data to his, not testing them. However, ours give his observations on *Larinioides cornutus* an extra dimension. Our observations also

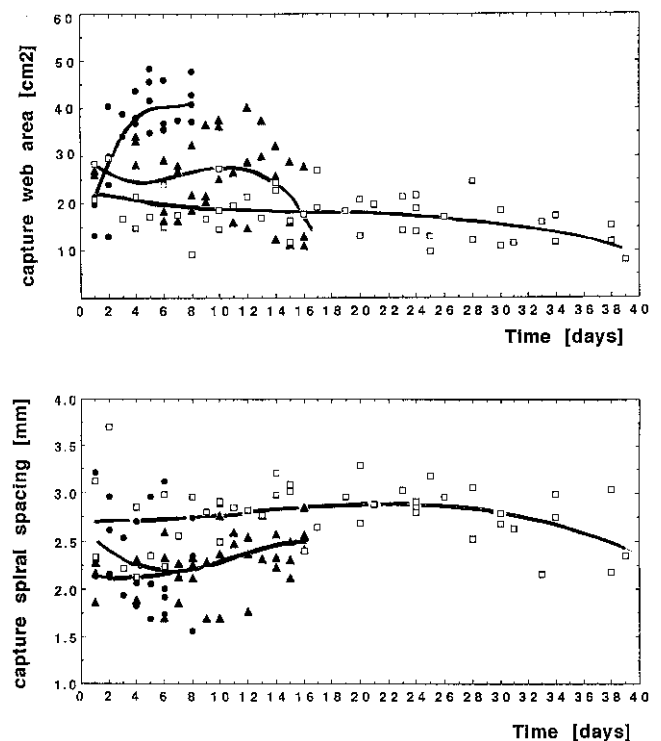


Fig. 2: Capture area and spiral spacing of *Araneus diadematus* webs built during the different feeding treatments. We show 3rd order polynomial regression curves for each treatment dataset containing the subsequent webs of 4 individual spiders per treatment: satiation (black circles), 1 fly daily (black triangles), starvation (white squares). Correlations were for web area (upper graph): satiation (upper curve, $r^2=0.663$), 1 fly daily (middle curve, $r^2=0.146$) and starvation (lower curve, $r^2=0.246$); and for spiral spacing (lower graph): satiation (middle curve, $r^2=0.073$), 1 fly daily (lower curve, $r^2=0.187$) and starvation (upper curve, $r^2=0.113$). Note that spiders fed to satiation (10 flies daily) moulted after about day 9 and therefore were truncated at day 8, normally fed spiders (1 fly daily) moulted after about 18 days and were truncated at day 16, starving spiders did not moult. Treatment began at day 0.

indicated that the web geometry of a typical orb weaver can be rather variable, although this variability may need considerable investigation to be uncovered fully. In this respect our results of the “normal to starvation” diet were revealing by suggesting that this rather drastic change in food intake had at first no measurable effect. Only very much later, in the last few days of the treatment, did it show a discernible effect on capture area without any visible effect on web mesh. Even the effect on capture area was non-significant in the context of the whole experiment, although it could be magnified with selective statistics (i.e. comparing only the first 6 with the last 6 days and ignoring the days in between, Fig. 2, top).

Finally, our observations agree with Sherman's observations on the high individual variability of spider web-building patterns on subsequent days; we also agree

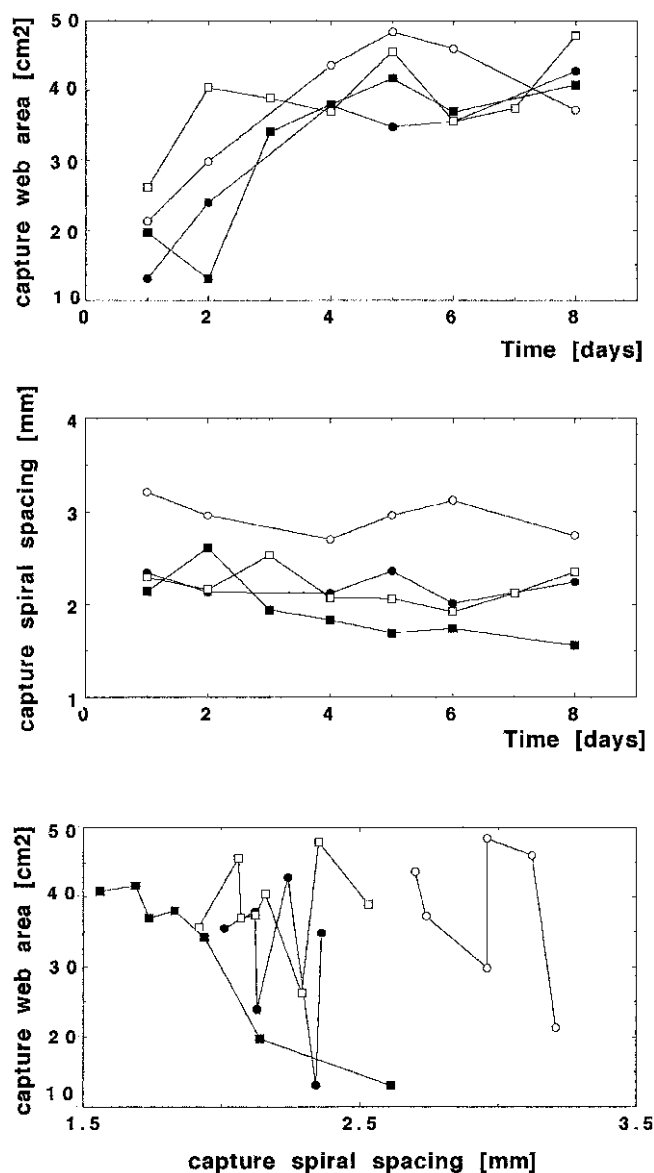


Fig. 3: Variability in web parameters in well fed *Araneus diadematus*. The spiders were on the satiation treatment (10 flies daily) and show in higher resolution and interconnected the “rich diet” data also plotted in Fig. 2. Each line shows the data from one spider. The bottom graph shows that there is obviously no correlation between spiral spacing and web area.

with his conclusions about the difficulties this poses for any study of orb-spider web geometry. Indeed, because of our much more controlled environmental and dietary conditions, our observations (Fig. 3) strongly underline Sherman's. However, we also note that the level of individual variability on subsequent days seemed higher in starving than in control or over-fed spiders. Comparing the day to day variability in web area and mesh size we found that the webs of individual spiders on the rich diet showed a clear (and significant) trend but less variability in subsequent webs, whereas those on either low or starvation diet generally varied considerably on subsequent days but showed no significant trend over the total period. This suggests that any study aiming to unravel the spider's web geometry (and by extension its building behaviour) needs to ensure that housing and diet are well controlled.

Summarising our observations we may say that a decrease in prey led to an increase in the frequency of web-building activity as well as a high level of variability in web geometry (mesh and capture area). An increase in prey, on the other hand, led to a decrease in web-building frequency and seems to have brought about the behavioural response of web fine-tuning (by increasing capture area). Since it has been shown that web-building activity and web geometry can be highly interrelated (Eberhard, 1982; Vollrath *et al.*, submit.), any detailed and statistical study of the phenomenon of web fine-tuning must also unravel this interrelation. Our data, on the whole, support the notion that spiders may be capable of responding to changes in prey availability by adjusting the architecture of their webs, although this is well within the limits of a naturally occurring, and seemingly random, variability of the measured parameters which, in turn, can be linked directly to prey capture efficiency (Eberhard, 1986; Rhisiart & Vollrath, 1994).

References

- DISJONVAL, Q. 1797: *L'Aranéologie*. 1–164. J.J. Fuchs, Paris.
- EBERHARD, W. G. 1982: Behavioral characters for the higher classification of orb-weaving spiders. *Evolution* **36**: 1067–1095.
- EBERHARD, W. G. 1986: Effects of orb-web geometry on prey interception and retention. In W. Shear (ed.), *Spiders, webs, behavior and evolution*: 70–100. Stanford, Stanford University Press.
- ENDERS, F. 1977: Web-site selection by orb-weaver spiders, particularly *Argiope aurantia* Lucas. *Anim. Behav.* **25**: 694–712.
- JANETOS, A. C. 1982: Foraging tactics of two guilds of web-spinning spiders. *Behav. Ecol. Sociobiol.* **10**: 19–27.
- JANETOS, A. 1986: Web site selection: are we asking the right questions? In W. Shear (ed.), *Spiders, webs, behavior and evolution*: 9–22. Stanford, Stanford University Press.
- LEBORGNE, R., PASQUET, A. & SEBRIER, M.-A. 1991: Modalities of feeding behaviour in an orb-weaving spider *Zygiella x-notata* (Clerck) (Araneae: Araneidae). *Behaviour* **117**: 206–219.
- OLIVE, C. W. 1982: Behavioral response of a sit-and-wait predator to spatial variation in foraging gain. *Ecology* **63**: 912–920.
- PASQUET, A., RIDWAN, A. & LEBORGNE, R. 1994: Presence of potential prey affects web-building in an orb-weaving spider *Zygiella x-notata*. *Anim. Behav.* **47**: 477–480.
- RHISIART, A. ap & VOLLRATH, F. 1994: Design features of a spider's orb web. *Behav. Ecol.* **5**: 280–287.

- SAMU, F. & VOLLRATH, F. 1992: Spider orb web as bioassay for pesticide side effects. *Entomologia exp. appl.* **62**: 117–124.
- 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.
- SPILLER, D. A. 1992: Numerical response to prey abundance by *Zygiella x-notata* (Araneae, Araneidae). *J. Arachnol.* **20**: 179–188.
- VOLLRATH, F. 1985: Web spider's dilemma: risky move or site dependent growth. *Oecologia* **68**: 69–72.
- VOLLRATH, F. 1987: Foraging, growth and reproductive success. In W. Nentwig (ed.), *Ecophysiology of spiders*: 357–370. Springer, Heidelberg.
- VOLLRATH, F. 1988: Deducing habitat quality from spider growth. *Bull. Br. arachnol. Soc.* **7**: 217–219.
- VOLLRATH, F., DOWNES, M. & KRACKOW, S. submit. Design variables in the orb web of the spider *Araneus diadematus*. *Oikos*.
- VOLLRATH, F. & HOUSTON, A. 1986: Previous experience and site tenacity in the orb spider *Nephila clavipes*. *Oecologia* **70**: 305–308.
- WITT, P. N., REED, C. F. & PEAKALL, D. B. 1968: *A spider's web: problems in regulatory biology*. Springer, New York.

Bull. Br. arachnol. Soc. (1997) **10** (8), 298–302

Carorita limnaea (Araneae: Linyphiidae) and other Araneae at Wybunbury Moss, Cheshire — a unique refuge for two relict species of spider in Britain

C. Felton and S. Judd

Zoology Department,
Liverpool Museum,
William Brown Street,
Liverpool L3 8EN

Summary

The distribution of the endangered, British Red Data Book status 1, linyphiid spider, *Carorita limnaea* (Crosby & Bishop) is described at Wybunbury Moss, Cheshire. *C. limnaea* was not recorded during a survey of ten other schwingmoors in Cheshire, Shropshire, Staffordshire and Clwyd. Both it and *Gnaphosa nigerrima* L. Koch are relict species, apparently restricted in Britain to Wybunbury Moss. One hundred and thirty-three spider species are recorded from the site. Eleven species of harvestmen and one pseudoscorpion are also recorded.

Introduction

In 1994 English Nature funded a Liverpool Museum survey to determine the status and conservation requirements of *Carorita limnaea*, a minute linyphiid spider known in Britain only from Wybunbury Moss, Cheshire (Grid ref. SJ 697503). It was first recorded there in 1962 (Duffey & Merrett, 1963) and subsequently by J. R. Parker in 1970 and C. Fulton in 1982 (English Nature, 1991), and S. Dobson and J. D. Stanney in 1993 (Scott, 1993). The possible threats to its survival at this site were briefly summarised by Merrett (1991).

Little is known about the biology of this species. It is rare throughout its extensive Holarctic range and is recorded from the United States, Belgium, Germany, Sweden and Finland (Duffey & Merrett, 1963) and recently, from a number of river basin sites in north-east Asia (Marusik, Eskov & Kim, 1992), and Canada and throughout northern Asia (see Eskov, 1994).

The site

Wybunbury Moss is a National Nature Reserve (NNR) and a Site of Special Scientific Interest which is given Grade 1 Status in the British Nature Conservation Review (Ratcliffe, 1977). It is positioned almost centrally in the recently designated Midlands Meres and Mosses Ramsar Site and is one of the two best examples of schwingmoor in the British Isles (English Nature, 1991). Chartley Moss NNR, Staffordshire (Grid ref. SK02-28-) and Wybunbury Moss are “subsidence raised mires” and are structurally unique in Britain. They are of great scientific importance within a national and a European context (English Nature, 1991).

The Reserve is small (11.43 ha), very compact, with different habitats compressed together, and is surrounded by 3.8 ha of wet pasture, which is also managed by English Nature. It is not contiguous with any areas of known ecological importance, being isolated in an agricultural and urban landscape.

Four major plant communities occur in the Reserve — *Sphagnum* lawn; pine woodland; fen woodland; and mixed birch, oak, and rowan woodland (Poore & Walker, 1958; Green & Pearson, 1968). These, together with the surrounding wet grassland were most recently mapped in the site management plan (English Nature, 1991). The post-glacial history of the site was discussed by Green & Pearson (1977).

Its small size and isolation make the site vulnerable, particularly to run-off water containing fertiliser from surrounding agricultural land and until recently, to eutrophic water from adjacent houses. This pollution extends across nearly two-thirds of the site and has led to the deterioration of the surface-floating peat raft and in several places to its collapse and also to the spread of rheophilous mire communities (Rieley & Page, 1990). This is a potential threat to *C. limnaea* and other spiders.

Recent management at the site has included the reversal of the successional advancement of pine/birch woodland on the *Sphagnum* lawn and the successful instalment of a pumped drainage system to stop household pollution.