

## The effect of leg loss on orb-spider growth

Monika Weissmann and Fritz Vollrath\*

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

### Summary

Adult *Zygiella x-notata* which lost legs early in life were lighter but not smaller than fully intact spiders. This difference was significant in several poor habitats but not in a rich habitat.

### Introduction

Field studies show that spiders are rather prone to losing a leg. Oppenheim (1908) estimated that up to 70% of spiders lose a leg during their lifetime. Friedrich (1906) found that 30% of all his collected spiders had lost at least one leg (no species names given). Among orb spiders, we found (unpublished observations) that 10% of a specific Isles of Scilly population of *Araneus diadematus* Clerck had lost one or two legs ( $n=100$ ); in a specific Panama population of subadult female *Nephila clavipes* (L.) it was 21% ( $n=100$ ). Both of these species sit at most times on the hub of their webs, exposed to predators. *Meta segmentata* (Clerck) and *Tetragnatha extensa* (L.) also sit on their webs, yet Oxford populations ( $n=100$  for each species) had not a single incomplete adult female. For *Zygiella x-notata* (Clerck), which spends most of the day in a retreat, a Scilly population ( $n=100$ ), interspersed with the *Araneus* population mentioned, showed 8% leg loss in September 1982, and pilot studies in Oxford showed the losses of legs to be 5% in August ( $n=100$ ) and 8% in December 1984 ( $n=100$ ). A few of the Scilly and Oxford spiders had even lost three legs. Last but not least, FV observed in the field in Panama an adult female *Nephila* with 5 missing legs building a web and catching prey, albeit clumsily. Note that *Nephila* and *Zygiella* autotomise but do not regenerate legs, *Meta* and *Tetragnatha* neither autotomise nor regenerate, and *Araneus* both autotomises and regenerates (Vollrath, 1990).

Observations on the geometry of a range of orb webs indicate that webs built with fewer than eight legs are smaller, more coarsely meshed and more uneven than webs built by intact spiders (Jacobi-Kleemann, 1953; Le Guelte, 1965; Reed *et al.*, 1965); a detailed study has shown that leg loss impairs certain aspects of the web-building behaviour (Weissmann & Vollrath, in prep. a). Furthermore, leg loss also affects prey capture behaviour directly by slowing the hunting spider down (Weissmann & Vollrath, in prep. b). These implications of leg loss on web structure and prey capture are likely to have an effect on the unfortunate spider's fitness. In this study we set out to quantify this effect by studying in the field the growth of spiders with 8 or fewer legs.

## Material and methods

The sector spider *Zygiella x-notata* (Araneidae) is common on man-made structures (e.g. window frames, fences, bridges) where it builds a smallish orb web of c. 20 cm diameter (Le Guelte, 1966). One pie-shaped sector of this orb is usually left free of capture spiral threads. A single thread traverses this sector and leads to the retreat, a silken tube hidden in a corner or crack. The spider spends most of its time in the retreat which it leaves to catch prey or to build a new web. Prey is transported to the retreat and eaten there. In Oxford, *Zygiella x-notata* eggs hatch in April–May, the first females moult to maturity in early August and the main egg-laying period ranges from October to December. Some adult females survive the winter and can be found until April.

*Zygiella* was chosen for this study because of an apparently strong site tenacity (Pasquet *et al.*, 1994), thought to be high for orb-spiders because of the retreat *Zygiella* always uses during the daytime (Marples & Marples, 1971). For ease of recapture we provided marked and numbered artificial retreats in several field localities with high incidences of *Zygiella*; the retreats were used to replace existing and occupied natural retreats. Each artificial retreat consisted of two numbered drinking straws (2 cm long, 4–5 mm diameter) one fitting snugly inside the other. The inner straw was used for transporting the spiders to the laboratory for weighing and marking. The system worked well enough in the laboratory; however, we found in the field that our spiders had very low site tenacity, i.e. they seemed to leave the artificial retreats after having been taken to the laboratory to be weighed, measured and marked. Immatures were never marked whereas all adult females were individually marked — dorsally on the pro- and opisthosoma, one fine dot each of fast-drying Humbrol non-toxic enamel. This method apparently does not harm the spiders (Vollrath & Rohde-Arndt, 1983); however, dots can fall off when a spider feeds well and the abdomen expands.

For our study we used four field sites in Oxford: an old vicarage street-fence, a fence next to a stream, our departmental playing-field fences and, finally, a subway underpass (tunnel) under the ring-road. All fences were similar in structure to one another but had different exposures to wind and sun. The stream site was divided into two treatments (left and right bank). The tunnel was sheltered and had high prey densities near the lights where the webs were clustered.

In the first census (late July/early August) all spiders in these four sites were caught into the numbered straws and their positions marked with the same numbers. After weighing (to the nearest 0.1 mg) and measuring (length of patella+tibia I to nearest 0.05 mm under a stereo-microscope) all spiders in the laboratory, they were returned in their transport straws, and the straws fixed at each marked site and opened a few hours later. After the second census (mid/late August) 146 of the juvenile spiders caught were made to autotomise legs (in various combinations) by squeezing the femur of the

\*Corresponding author and present address: Department of Zoology, Universitetsparken B135, DK 8000 Aarhus C, Denmark.

anaesthetised spider with forceps (Vollrath, 1990), the other 218 spiders being left as controls. All adult females found during the 2nd census were marked ( $n=82$ ). A final census was done in the second half of September.

It emerged during our study that in the field *Zygiella* did not remain in the artificial retreats (either they moved out or were heavily preyed upon); our recapture rate was as low as 2 of 82 marked individuals. Thus we had to rely more than planned on the weight and size data collected during the study, rather than the recapture data which would have given much more detailed data.

## Results

During the study period July to September, the incidence of leg loss increased dramatically (from 4.2% to 12%); this included spiders missing more than one leg (an increase from 0.5% to 8%). During the two-month observation period the combined mortality and emigration at the 4 sites was 23% of the total ( $n=449$ ) of all spiders censused with, surprisingly, zero mortality/emigration in the tunnel.

We noted during the July and August censuses that the different sites had similar proportions of naturally missing legs: vicarage fence ( $n=56$ ): 3.6%, stream path fence (left  $n=114$ , right  $n=122$ ): 2.7 and 4% respectively, zoology fence ( $n=78$ ): 9%, tunnel ( $n=79$ ): 2.5%. A combined sample ( $n=640$ ) taken during that time which included 3 other sites ( $n=191$ ) in addition to the 4 focal sites ( $n=449$ ) showed that 1st legs were more vulnerable (2.8%) than 2nd legs (0.5%), 3rd legs (0.3%) or 4th legs (0.8%). In addition one spider lacked both first legs, another spider lacked both second legs and three spiders lacked the 1st and 2nd leg on the same side.

The calculations of body reserves (i.e. the ratio of weight to size based on data from the last census) for freshly moulted individuals of all sizes showed that spiders in the tunnel site must have experienced a better nutritional quality than spiders in any of the other 3 "outdoor" sites. The tunnel spiders were significantly better fed (heavier) than spiders from any fence site, and the three fence sites did not differ from one another (ANOVA  $F_{3,66}=13.50$ ). We therefore combined the data from the three fence sites for the next analysis. Here we found that in the fence sites mature females with missing legs (ML,  $n=14$ ) were significantly lighter than intact females (OK,  $n=25$ ) (ML vs. OK =  $28.8 \pm 12.3$  mg vs.  $43.9 \pm 22.9$  mg;  $F=4.8$ ,  $p<0.05$ ) although they were not significantly smaller ( $3.92 \pm 0.17$  mm vs.  $3.99 \pm 0.22$  mm;  $F=1.15$ , n.s.). In the tunnel site we found no significant differences between females with missing legs ( $n=24$ ) and intact ones ( $n=35$ ); they were rather similar in weight ( $56.6 \pm 24.7$  mg vs.  $60.3 \pm 29.5$  mg) and size ( $4.13 \pm 0.35$  mm vs.  $4.01 \pm 0.48$  mm).

## Discussion

The results of our study suggest that in most natural habitats losing one or several legs is a serious handicap

because it can lead to a significant reduction in foraging success, i.e. reduced weight gain. In a rich and apparently protected habitat (like the tunnel) this effect may not be pronounced. Our data suggest that in the tunnel prey were rather abundant, so abundant that even handicapped spiders got their fill. However, this would be a highly unusual situation for spiders in the field, be they hunters (e.g. Miyashita, 1968) or web spinners (e.g. Wise, 1975; Vollrath, 1988; Pasquet & Leborgne, 1990) because typically prey availability would limit growth (Vollrath, 1987).

Our experiments were conducted with *Zygiella*, since this spider's habits were supposed to enable individual follow-ups of leg-loss early in life (consistent recaptures). On the one hand our marking method could have been inadequate; we suspect that paint dots were shed by the expanding abdomen. Moreover, we also suspect that the spiders were more mobile than expected. This mobility was probably caused by behavioural factors such as aggressive interactions after release (Kremer *et al.*, 1987; Leborgne & Pasquet, 1987a,b) and responses to prey quality of a site considered new after release (Leborgne *et al.*, 1991; Pasquet *et al.*, 1994). Whatever the cause, the unexpected problems with marking and mobility severely limited our sample size and thus constrained our results.

Nevertheless, our data show conclusively that leg loss has an effect on predatory success and thus life history parameters. In the poorer (and more natural) sites the "leg loss" spiders were significantly lighter than the intact spiders. Extrapolating from these data to the influence on a spider's reproductive fitness may be possible; we can assume that the less well nourished "leg loss" females would find it more difficult to build up good/sufficient reserves to lay eggs before the winter. Thus, on balance, we concluded that loss of even one leg would normally constitute a handicap. We note that it is therefore curious that neither *Zygiella* (nor, apparently, other tetragnathids) regenerate lost legs (Vollrath, 1990). *Araneus*, like most other spiders (orb weavers or not), does regenerate and it seems that the loss of regeneration is an apomorphic trait (Vollrath, 1990). It has been suggested that the suppression of regeneration might be a trait linked to an inability of some spiders to incorporate any newly regenerated (and therefore much shorter) legs into the complex behaviour pattern of web-building (Vollrath, 1995).

The predatory success of a spider depends on a variety of variables, some of which show significant declines when a spider loses legs. Prey capture experiments with leg loss in *Nephila* (Weissmann & Vollrath, in prep. a, b) confirmed that there is a complex interaction with spider handicap during both web-construction (web-building impaired) and prey-capture (running orientation impaired). We assume that the relatively lighter weight of "leg loss" *Zygiella* in the field might have been caused by a combination of these factors and that the spiders could not compensate perfectly for missing legs. After all, in *Zygiella* leg loss leads to reduced web regularity (Weissmann & Vollrath, in prep. b), and spiral regularity and spacing have been identified as important

factors in capture success (Eberhard, 1986; Rhisiart & Vollrath, 1992).

### Acknowledgements

We thank Richard Dawkins for continued support and advice and Peter Merrett for much helpful critique; MW thanks the Queen's College Oxford for awarding her the Florey studentship and Peter Merrett for a perceptive M. Sc. examination; FV thanks the SERC for a research fellowship.

### References

- EBERHARD, W. G. 1986: Effects of orb-web geometry on prey interception and retention. In W. A. Shear (ed.), *Spiders, webs, behavior and evolution*: 70–100. Stanford University Press.
- FRIEDRICH, P. 1906: Regeneration der Beine und Autotomie bei Spinnen. *Arch. Entw.-Mech. Org.* **20**: 469–506.
- JACOBI-KLEEMANN, M. 1953: Über die Lokomotion der Kreuzspinne *Aranea diademata* beim Netzbau (nach Filmanalysen). *Z. vergl. Physiol.* **34**: 606–654.
- KREMER, P., LEBORGNE, R., PASQUET, A. & KRAFFT, B. 1987: Interactions entre femelles de *Zygiella x-notata* (Clerck) (Araneae, Araneidae): influence sur la taille des toiles. *Biol. Behav.* **12**: 93–99.
- LEBORGNE, R. & PASQUET, A. 1987a: Influences of aggregative behaviour on space occupation in the spider *Zygiella x-notata* (Clerck). *Behav. Ecol. Sociobiol.* **20**: 203–208.
- LEBORGNE, R. & PASQUET, A. 1987b: Influence of conspecific silk-structures on the choice of a web-site by the spider *Zygiella x-notata* (Clerck). *Revue arachnol.* **7**: 85–90.
- 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.
- Le GUELTE, L. 1965: Repercussions de la perte de pattes sur la construction de la toile chez *Araneus diadematus* et *Zygiella x-notata*. *Psychol. Fr.* **10**: 257–264.
- Le GUELTE, L. 1966: *Structure de la toile de Zygiella x-notata Clerck et facteurs qui régissent le comportement de l'araignée pendant la construction de la toile*. Doctorate thesis, Université de Nancy.
- MARPLES, B. J. & MARPLES, M. J. 1971: Notes on the behaviour of spiders in the genus *Zygiella*. *Bull. Br. arachnol. Soc.* **2**: 16–17.
- MIYASHITA, K. 1968: Growth and development of *Lycosa T-insignita* Boes. et Str. (Araneae: Lycosidae) under different feeding conditions. *Appl. Ent. Zool. Tokyo* **3**: 81–88.
- OPPENHEIM, S. 1908: Regeneration und Autotomie bei Spinnen. *Zool. Anz.* **33**: 56–60.
- PASQUET, A. & LEBORGNE, R. 1990: Prey capture efficiency and prey selection from insects intercepted by trap in four orb-weaving spider species. *Acta. oecol.* **11**: 513–523.
- 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. & VOLLRATH, F. 1994: Design features of a spider's orb web. *Behav. Ecol.* **5**: 280–287.
- REED, C. F., WITT, P. N. & JONES, R. L. 1965: The measuring function of the first legs of *Araneus diadematus* Cl. *Behaviour* **25**: 98–119.
- VOLLRATH, F. 1987: Growth, foraging and reproductive success. In W. Nentwig (ed.), *Ecophysiology of spiders*: 357–370. Springer, Berlin.
- VOLLRATH, F. 1988: Spider growth as an indicator of habitat quality. *Bull. Br. arachnol. Soc.* **7**: 217–219.
- VOLLRATH, F. 1990: Leg regeneration in web spiders and its implications for orb weaver phylogeny. *Bull. Br. arachnol. Soc.* **8**: 177–184.
- VOLLRATH, F. 1995: Lyriform organs on regenerated spider legs. *Bull. Br. arachnol. Soc.* **10**: 115–118.
- VOLLRATH, F. & ROHDE-ARNDT, D. 1983: Prey capture and feeding in the social spider *Anelosimus eximius*. *Z. Tierpsychol.* **61**: 334–340.
- WEISSMANN, M. & VOLLRATH, F. in prep. a: The effect of leg loss on an orb spider's web construction.
- WEISSMANN, M. & VOLLRATH, F. in prep. b: The effect of leg loss on a web spider's prey catching behaviour.
- WISE, D. H. 1975: Food limitation of the spider *Linyphia marginata*: experimental field studies. *Ecology, Brooklyn* **56**: 637–646.