Spider manipulation by a wasp larva*

A parasitic wasp forces its host to weave a special web for its own ends.

On the evening that it will kill its orb-weaving spider host, the larva of the ichneumonid wasp *Hymenoepimecis* sp. induces the spider to build an otherwise unique 'cocoon web' to serve as a durable support for the wasp larva's cocoon. The construction of this cocoon web is highly stereotyped, consisting of many repetitions that are almost identical to the early stages of one subroutine of normal orb weaving, the other components of which are repressed. Here I investigate this activity and show that the mechanism employed by the larva to manipulate the spider's behaviour is fast-acting, apparently chemical, and has long-term effects.

The female *Hymenoepimecis* sp. wasp attacks the spider *Plesiometa argyra* at the hub of its orb, stings it into temporary paralysis and lays an egg on the spider's abdomen[1]. Subsequently, the spider resumes normal activity. During the next 7-14 days, it builds apparently normal orbs (Fig. la) to capture prey, while the wasp's egg hatches and the larva grows by sucking the spider's haemolymph. On the night that it will kill its host, the larva induces the spider to build a cocoon web, moults, kills and consumes the spider, and then spins its pupal cocoon hanging by a line from the cocoon web.

Apparently undamaged cocoon webs almost always had several lines (mean, 3.8:f: 1.4; range, 2-8; *n=39)* radiating in a plane from a 'hub' (Fig. lb-f). Most radial lines branched near their tips and were attached to the substrate at many points (Fig. lb). Most webs had only radii and lines connecting them at the hub, and lacked circular hub lines (86% of 66) or frame lines (65% of 77) connecting the radial lines. Any frame lines present were typically much shorter and nearer the hub than those of normal orbs (Fig. le). The central portion of the hub was never empty, as it is in a normal orb (Fig. la). The most elaborate cocoon webs, however, had distinct hub loops, frames, and a mesh above and below the hub (Fig. lg), confirming that they were modified orbs.

The construction of cocoon webs was very consistent, and it appeared to be the same as the early stages of type 'D' frame construction (ref. 2, and W.G.E., manuscript in preparation). Many other integral features of normal orb-web construction, including breaking and then reeling up and replacing lines, and breaking and then re-attaching lines[2-6], were completely absent. A single 'mistake' in this respect by the spider could be disastrous for the wasp larva, as the many-stranded cable of radial lines would be replaced with a single pair of drag lines.

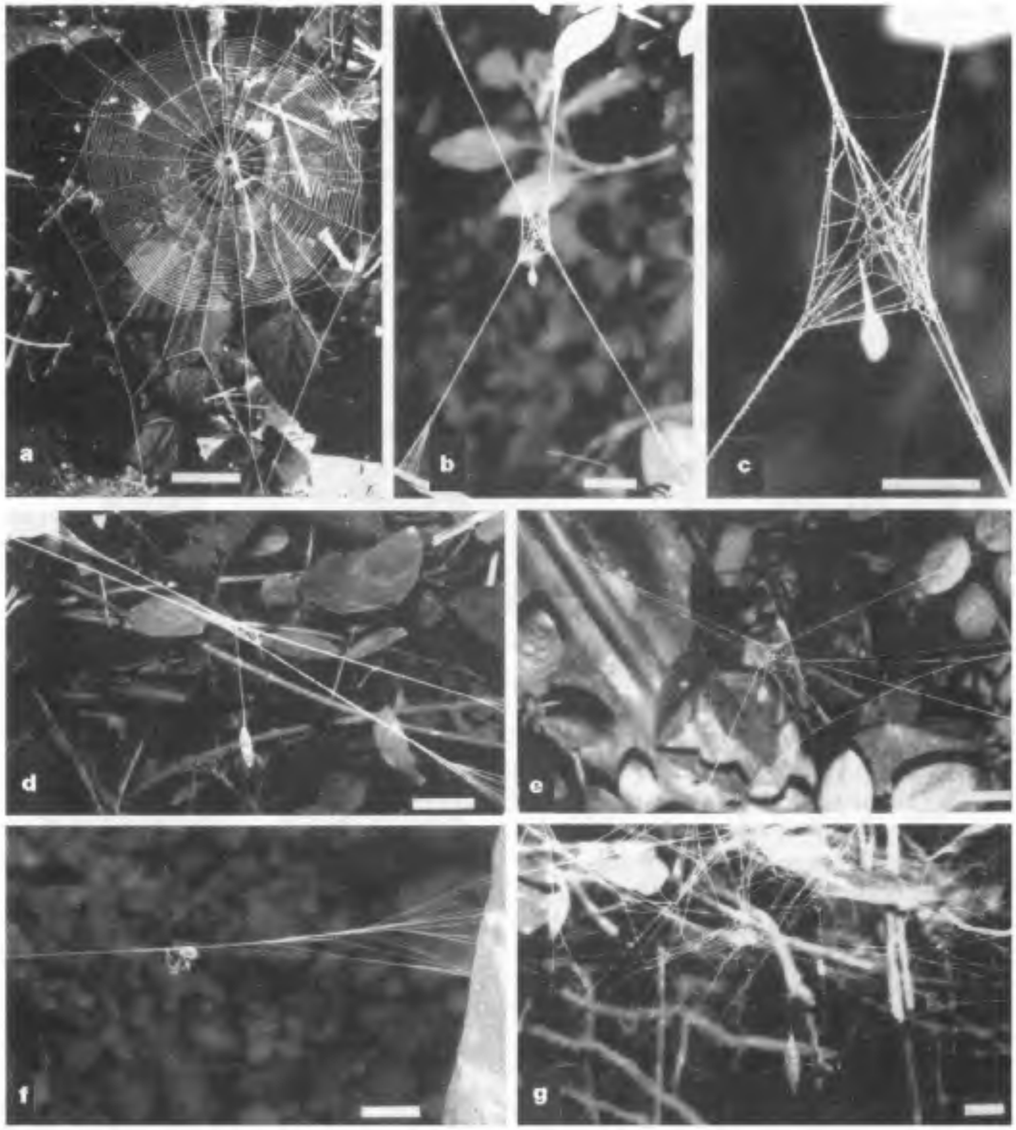

Figure 1 Webs of the orb-weaving spider *Plesiometa argyra*. **a.** Prey-capture orb of a mature female; **b.** cocoon web and wasp cocoon from above; **c.** hub of the cocoon web; **d.** cocoon web and cocoon from the side; **e.** cocoon web with one frame line; **f.** the simplest cocoon web, with only two radial lines (larva rests at the hub, consuming the dead spider); **g.** the most complex cocoon web, with circular lines at the hub and a mesh above and below the radial lines. Scale bars for a-g are 4, 2, 1, 2, 2, 2 and 2 cm. respectively.

The temporary and sticky spirals were also missing, and the central portion of the finished hub was not removed[2-6]. These differences between cocoon webs and normal orbs all make the cocoon web a stronger, more durable support for the wasp's cocoon. The importance of this is illustrated by the vulnerability of pupae of the related wasp *H. robertsae* to heavy rains[7].

The larva makes small holes in the spider's abdomen to imbibe haemolymph[1]. As the spider continues to build the cocoon web even when the larva is removed shortly before construction would normally start, the changes in the spider's behaviour must be induced chemically rather than by direct physical interference. The effects are both rapid (removal earlier in the evening did not result in the formation of typical cocoon webs) and long-lasting (spiders from which larvae were removed built similar webs the following night, although some slowly reverted to more normal orbs on subsequent nights).

The larva's ability to induce specific behaviour patterns in the spider indicates that, at some level within the host, such fine behavioural details are independent units, and not artificial constructs. This point is crucial in the use of behavioural patterns as taxonomic characters[8,9].

Many parasites manipulate their host's behaviour[10-13], but most of them, particularly insect parasitoids, induce only simple changes, such as movement from one habitat to another, eating more or less, or sleeping[12,13]. These brief communications

changes may be instigated by relatively straightforward mechanisms, for example by the modification of particular receptors[14,15]. *Hymenoepimecis*'s manipulation of its spider host is probably the most finely directed alteration of behaviour ever attributed to an insect parasitoid.

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1. Eberhard, W. G. *I. Hymen. Res.* (in the press).
2. Eberhard, W. G. ,. *Arachnol.18,* 205-234 (1990).
3. Tilquin, A. *La Toile Géometrique* des *Araignées* (Presses Univ. France, Paris, 1942).
4. Eberhard, W.G. *Evolution* 36, 1067-1095 (1987).
5. Coddington, I. A. in *Spiders- Webs, Behavior and Evolution* (ed. Shear, W.) 319-363 (Stanford Univ. Press, Palo Alto, CA, 1986).
6. Witt, P. N., Reed, c. & Peakall, D. B. A Spider's Web (Springer, New York,1968).
7. Fincke, 0., Higgins, L. & Rojas, *E.I. Arachnol.* 18, 321-329 (1990).
8. Griswold, c. E., Coddington, J. A., Hormiga, G. & Scharff, N. *Zool. J. Linn. Soc.* 123, 1-99 (1998).
9. Wenzel, J. W. *Annu.* Rev. *Ecol. Syst.* 23, 361-381 (1992).
10. Holmes, J. C. & Bethel, W. M. in *Behavioural Aspects of Parasite Transmission* (eds Channing, E. U. & Wright, C. A.) 123-149 (Academic, London, 1972).
11. Barnard, C. J. & Behnke, J. M. *Parasitism and Host Behaviour* (Taylor & Francis, London, 1990).
12. Toft, C. A., Aeschlimann, A. & Bolis, L. *Parasite-Host Associations* (Oxford Univ. Press, New York, 1991).
13. Godfray, H. C. J. *Parasitoids. Behavioral and Evolutionary Ecology* (Princeton Univ. Press, Princeton, NJ, 1994).
14. Jenni, L., Molyneux, D. H., Livesey, J. L. & Galun, R. *Nature* 283, 383-38S (1980).
15. Wickler, W. Z. *Tierpsychologie 42,* 200-214 (1976).