

LETTER

Are three-dimensional spider webs defensive adaptations?

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Abstract

Spider webs result from complex behaviours that have evolved under many selective pressures. Webs have been primarily considered to be foraging adaptations, neglecting the potential role of predation risk in the evolution of web architecture. The ecological success of spiders has been attributed to key innovations in how spiders use silk to capture prey, especially the invention of chemically adhesive aerial two-dimensional orb webs. However, araneoid sheet web weavers transformed the orb architecture into three-dimensional webs and are the dominant group of aerial web-building spiders world-wide, both in numbers and described species diversity. We argue that mud-dauber wasps are major predators of orbicularian spiders, and exert a directional selective pressure to construct three-dimensional webs such that three-dimensional webs are partly defensive innovations. Furthermore, patterns of diversification suggest that escape from wasp predators may have facilitated diversification of three-dimensional web-building spiders.

Keywords

Adaptive radiation, Araneidae, key innovation, Linyphiidae, orb web, sheet web, silk, Sphecidae, Theridiidae.

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INTRODUCTION

Diversification of arthropods and their subsequent dominance of earth's biodiversity have been attributed to shifts and expansions in exploitation of food (Ehrlich & Raven 1964; Farrell & Mitter 1994). Within spiders, whose 37 000+ described species are all predators of arthropods, innovations in the use of silk in foraging, such as chemically adhesive two-dimensional (2-D) orb webs, may have been especially important (Bond & Opell 1998). Aerial orb webs allow exploitation of abundant flying insects, require little silk, and allow spiders to change foraging patches efficiently through recycling of silk (Janetos 1982; Shear 1986).

However, 2-D orb weaving is an ancient behaviour (Coddington & Levi 1991; Griswold *et al.* 1998), and the araneoid sheet web weavers have transformed the orb architecture into typically three-dimensional (3-D) sheet or tangle webs (Fig. 1; Coddington & Levi 1991; Griswold *et al.* 1998). This change is associated with a 43% increase in described species diversity of araneoid sheet web weavers (Platnick 2001) and a 400% increase in numerical abundance in ecosystems across the world (see below). 3-D webs are not recycled daily, constraining spider mobility (Janetos

1982), but may better protect spiders against predators (see below).

Construction of spider webs involves a complex series of behaviours that have evolved under many selective factors, among which predation risk has received little consideration. Here, we examine the hypothesis that 3-D webs may be adaptations against predation by mud-dauber wasps that specialize upon spiders in the Orbicularia.

METHODS

Six sphecid genera hunt spiders exclusively (Bohart & Menke 1976), capture 20 or more spiders daily for larval food (Coville 1987; Rayor 1997; Blackledge & Wenzel 2001), and occur in most terrestrial ecosystems. Because paralysed spiders can be recovered from wasp nests, selection on spider defensive behaviours can be elucidated by comparing behavioural phenotypes of prey with the background frequency of spiders in the habitat.

We compiled all known captures of spiders by sphecid wasps from studies published over the last century. These studies encompassed a variety of ecosystems from around the world. Several techniques were used to collect wasp prey, mainly excavation of provisioned prey from natural

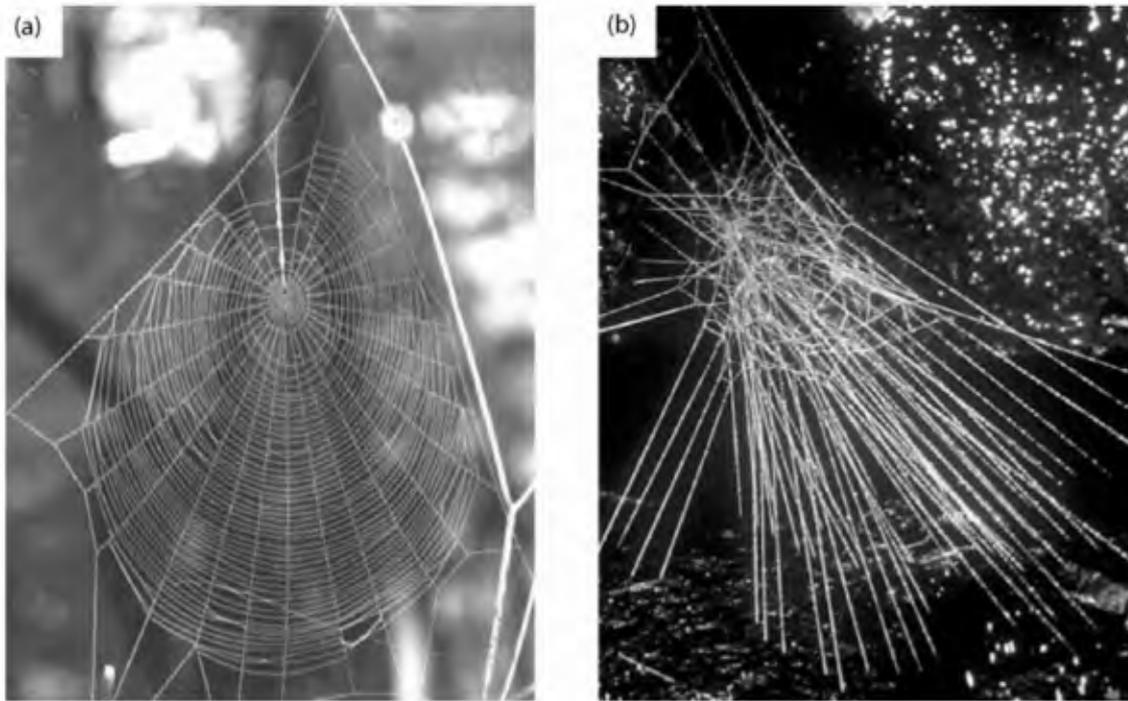


Figure 1 Two types of aerial spider webs. (a) Two-dimensional orb webs provide spiders with very efficient traps to capture flying insects and the silk is easily recycled from day to day. However, orb-weaving spiders must rest either at the centres of webs where spiders are vulnerable visually and physically to predators or in retreats next to webs. (b) The 'araneoid sheet web weavers' build three-dimensional sheet or tangle webs. These relatively permanent webs surround spiders with three-dimensional networks of silk that can give advanced warning about attacks by predators or physically block predators.

and wooden trap nests, but also opportunistic observations on burrow-nesting taxa. These data collectively provide the best available evidence on the threat predatory wasps pose to spiders, but are biased in various ways, particularly by discrepancies in sample sizes between wasp genera. However, within each genus the relative frequencies of spider behavioural phenotypes probably reflect wasp prey preferences with reasonable accuracy.

We used faunal surveys to estimate background frequencies of behavioural phenotypes of potential spider prey. Fifty percent of surveys (70% of all data), used standardized techniques, including direct searching, beating, sweeping, pitfall trapping, canopy fogging, and litter sifting (see Coddington *et al.* 1991, 1996; Sorensen *et al.* 2002 for methodology). These methods are not ideal for estimating relative abundances of spiders, but are probably least biased within web-building spiders at shrub, herb and ground levels, which is the comparison of interest here. We classified spiders into three behavioural phenotypes (Figs 1 and 2b). (1) 3-D web-builders included a single apomorphic clade within the Orbiculariae, the 'araneoid sheet web weavers', which construct diverse but usually highly three-dimensional webs. (2) 2-D web-builders included all other orbicularian taxa that retain plesiomorphic orb webs. (3)

Other spiders included non-orbicularian taxa from 24 families, of which only Agelenidae (4 prey), Dictynidae (197 prey), and Pholcidae (18 prey) typically build webs.

RESULTS

We recorded 30 375 records of identified spider prey from 70 publications (130 observations differentiated by wasp species and/or localities) and 164 118 records of potential prey available in habitats from 26 faunal surveys. Aerial web-building orbicularians comprised 76% of all prey (Table 1), most of which built the ancestral 2-D orb architectures (Table 1 and Fig. 2a). Araneoid sheet web weavers, with their 3-D web architecture, accounted for only 17% of predation within the Orbiculariae, even though these spiders constitute 81% of the numerical abundance and 59% of species diversity within the Orbiculariae (Fig. 2a). Wasps captured more orb-weavers than araneoid sheet web weavers in 86 of 111 studies (sign test $P < 0.0001$; 19 studies lacked orbicularian taxa), even though sheet web weavers were more abundant in 21 of 26 faunal surveys (sign test $P < 0.005$). There was a significant difference in the numbers of 2-D vs. 3-D web weaving spiders in each study when comparing the prey captured by wasps and

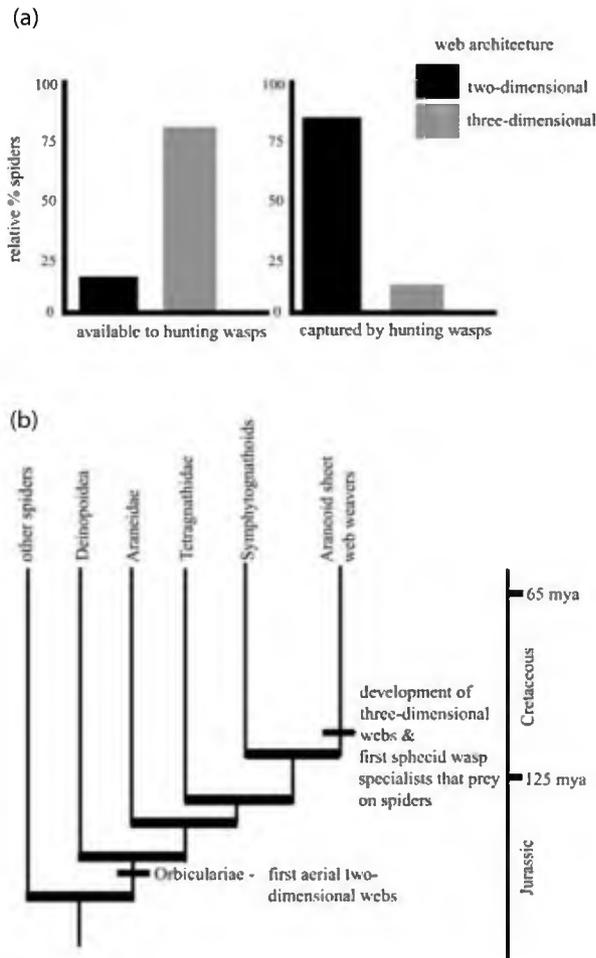


Figure 2 Wasps exert directional selection that favours three-dimensional web architectures. (a) ‘Araneoid sheet web weavers’ are 400% more abundant than ancestral orb-weaving spiders in the environment, but orb-weaving spiders are 476% more common as prey of wasps. Thus, predation by wasps exerts a directional selective force that favours the building of complex, three-dimensional webs. Collectively, 2- and 3-D web-building spiders constitute 76% of all prey captured by wasps. (b) Phylogenetic relationships within the Orbiculariae, based upon behavioural and morphological characters (Griswold *et al.* 1998). Orb-weaving spiders first evolved and diversified in the Jurassic, at least 125 mya (Selden 1989), prior to the appearance of predatory wasps in the early Cretaceous. It is only after the diversification of sphecid wasps in the mid to late Cretaceous (Bohart & Menke 1976) that the ‘araneoid sheet weavers clade’, with its three-dimensional web architecture, evolved from an orb-weaving ancestor and diversified in the Cretaceous and Cenozoic (Penney & Selden 2002).

available prey (Mann–Whitney *U*-test, $P < 0.000005$, using each sample listed in Appendices 1 and 2). Finally, four of the five genera of wasps, for which we have multiple prey records, captured 2-D web-building spiders at significantly higher frequencies than that estimated by faunal surveys

(*G*-tests, $P < 0.05$). Sphecid wasps are significantly biased towards two-dimensional orb weavers as prey.

DISCUSSION

No doubt three-dimensional web architectures influence many aspects of spider biology, which we cannot discuss or even begin to enumerate here. However, these data are consistent with the hypothesis that 3-D web architectures provide a defensive advantage against wasps compared to plesiomorphic 2-D orb webs. It is further plausible that 3-D web architecture may have originated in part due to selective pressures from wasps and that escape from wasp predation may have facilitated the evolutionary diversification of araneoid sheet web weavers. The role of predatory wasps in web-building spider evolution has not been considered heretofore.

Wasps are a significant danger to spiders

Invertebrates, such as sphecid wasps, are often primary predators of web-building spiders (Coville 1987; Blackledge & Wenzel 2001). Pompilid wasps capture up to 99% of adult burrowing wolf spiders (McQueen 1978). One study that considered multiple predatory taxa found that wasps (Pompilidae and Sphecidae) accounted for 93% of all attacks on colonial orb-weaving spiders in Mexico, with 500 h of observation yielding 465 attacks by 15 or more species of wasps (Rayor 1997). In small colonies, individuals risked a 1.5% chance of capture by wasps each day (Uetz & Hieber 1994). Finally, outbreaks of pompilid wasps reduced island populations of web-building spiders by 54–77% (Polis *et al.* 1998).

Birds also prey on spiders (e.g. Rypstra 1984; Gunnarsson 1996), but many studies have failed to find a significant impact of vertebrates upon spider densities (Polis *et al.* 1998; Wise & Chen 1999). Bristowe (1941) provided rough estimations of predation rates by common spider predators in England, from which we extrapolated that the 15 most abundant spider-consuming bird species collectively kill 2.9×10^{-4} spiders/m²/day. Bristowe does not provide similar figures for wasps, but the work of Freeman (1980) in the Caribbean does. We extrapolated that a single wasp species, *Sceliphron assimile*, captured 7.6×10^{-3} spiders/m²/day—30 times the total estimated for 15 species of birds in England. We know of no data that suggest that spider biomass in England is drastically less than on dry Caribbean islands. Furthermore, most birds capture primarily cursorial, rather than web-building, spiders (Bristowe 1941; Gunnarsson 1996; Burger *et al.* 1999). In contrast, sphecid wasps specialize on orbicularian web-building spiders, which constitute 75% of all prey in our study, with the next most abundant taxa, Thomisidae and Salticidae,

Table 1 Predation by spider hunting sphecids wasps in relationship to web architecture and availability of spiders in the environment. Taxa in the Orbiculariae are defined in Griswold *et al.* (1998). '3-D' web builders include only taxa in the 'araneoid sheet web weavers' clade, whereas the '2-D' web builders include all other clades within the Orbiculariae. 'Other' spiders includes all taxa outside the Orbiculariae. Unidentified taxa were omitted from the analysis due to lack of information about their behavioural phenotypes. Data from individual publications and full references are available in electronic Appendices 1 and 2

| Wasp genus | No. of studies | Geographical range | Orbicularian web architecture | | Other spiders |
|---|----------------|--|-------------------------------|--------|---------------|
| | | | 2-D | 3-D | |
| <i>Chalybion</i> | 7 | World-wide (except S. America) – 31 spp. | 1455 | 1826 | 70 |
| <i>Miscophus</i> | 13 | World-wide – 150 spp. | 7 | 241 | 162 |
| <i>Pison</i> | 8 | World-wide – 145 spp. | 52 | 46 | 853 |
| <i>Pisonopsis</i> | 1 | N. & S. America – 5 spp. | 1 | 40 | 0 |
| <i>Sceliphron</i> | 15 | World-wide – 30 spp. | 6448 | 104 | 2972 |
| <i>Trypaerylon</i> | 82 | World-wide – 359 spp. | 10 048 | 1419 | 3073 |
| Unidentified | 4 | | 964 | 304 | 290 |
| Total | 130 | | 18 975 | 3980 | 7420 |
| Availability of spider prey estimated by faunal surveys | 26 | World-wide (except Australia) | 20 224 | 80 706 | 63 188 |

comprising 17% of prey. Wasps are clearly very serious predators of web-building spiders.

Wasps exert a directional selective pressure that favours three-dimensional webs

Eighty-three percent of orbicularian spiders captured by wasps built 2-D webs, even though these taxa account for only 19% of the orbicularian spiders potentially available as prey in the environment. Thus, wasp predation could provide a directional selective force favouring construction of 3-D webs (Fig. 2a). Most araneoid sheet web weavers surround themselves with three-dimensional matrices of silk that can defend spiders in two ways. Physically, wasps must negotiate complex tangles of silk in 3-D webs, rather than attacking spiders directly on flat orb webs or in retreats next to webs (e.g. Eberhard 1970; Blackledge & Wenzel 2001). In addition, spiders in 3-D webs can gain early warning of attacks through vibrations transmitted via the silk. Such advantages have been demonstrated for some colonial orb-weaving spiders that construct interconnected webs (Uetz & Hieber 1994; Rayor 1997).

Although species vary (see Appendix 1), four of the six spider-hunting sphecids genera captured a lower proportion of 3-D to 2-D web-building spiders than predicted by available prey (Table 1), suggesting that preference for 2-D orb-weaving spiders may be relatively generalized. *Miscophus* and *Pisonopsis* both captured a higher proportion of 3-D web-building spiders than predicted by prey availability (Table 1), but those data included only a single study for *Pisonopsis*. Data on relative abundances of sphecids taxa are

lacking, but 2-D web specialists may also be more common, if the number of studies on each genus reflects wasp abundances more than ease of investigation (Table 1).

Alternative explanations

Complex evolutionary innovations such as the three-dimensional tangle or sheet web no doubt evolved for many reasons, and we do not suggest that wasp predation was the sole factor here. However, spider-specialist wasps take a large and notably biased fraction of web-building spiders, which should be considered in evolutionary explanations of spider web evolution. Webs are defensive as well as offensive structures. Alternatively, wasps generally exhibit size selectivity when capturing prey, and orb-weaving spiders tend to be larger as adults than sheet-web weavers (Kaston 1981; Hormiga *et al.* 2000). A potential preference by wasps for larger prey could explain the observed bias in taxonomic composition, but several lines of evidence argue against it. First, unlike pompilids, sphecids are less constrained by prey size, and capture spiders varying in mass by 1–2 orders of magnitude (Elgar & Jebb 1999; T.A. Blackledge unpubl.). Second, orb and 3-D web-building spiders overlap broadly in size as they mature from initially small juveniles, and many prey are immature spiders. Third, exclusion of the tiny litter-dwelling Linyphiidae does not qualitatively change these results. Finally, we included at least 67 species of wasps that vary widely in size and whose prey range from tiny immature to large adult female spiders (see Appendix 1). Although size selection may explain some of the disparity, it seems unlikely to be the major factor,

because wasps, in general, capture web-building spiders of all size classes.

Unlike 3-D webs, orb webs require as few as three attachment points to the substrate, allowing orb-weaving spiders to occupy more open microhabitats than other web spinners. Some sphecids hunt in open vegetation and might therefore tend to encounter more orb weavers (Blackledge & Pickett 2000; Blackledge & Wenzel 2001). Other sphecids, however, are quite adept at ferreting out spiders in small crevices (Eberhard 1970). Because our study summarizes the prey preferences for many wasp species, it should reflect the 'average' predatory pressure across microhabitats. Differences in web location are therefore unlikely to be a sufficient explanation for the wasp specialization on orb weavers. Furthermore, the tendency for sheet and tangle webs to be closer to substrates with more protected retreats could be an effect of wasp predation as much as an alternative explanation for the bias.

'Araneoid sheet web weavers' diversify after predatory wasps

Robust information on the timing of the relevant evolutionary events is lacking, but current data are consistent with 3-D spider web-architecture functioning as a defensive adaptation against predatory wasps (Fig. 2b). The major orb-weaving lineages within the Orbiculariae were present by the beginning of the Cretaceous (Selden 1989), and orb weaving probably originated at least 145 mya in the Jurassic (Selden 1989). Sphecids first appear by the Lower Cretaceous, and diversified by the end of the Cretaceous (65 mya; Bohart & Menke 1976). Araneoid sheet web weaving spiders, with 3-D web architectures, first appear by 130 mya in the Lower Cretaceous (Penney & Selden 2002; see also Penney 2002). These dates are roughly consistent with 3-D web-building behaviours evolving under selection from predatory wasps, although more data are clearly desirable.

Using a statistical, null Markovian model approach, Bond & Opell (1998) argued that diversification within the Araneae was generated primarily by adaptive radiations of several clades facilitated by key innovations, including the araneoid sheet web weavers. This suggests an additional hypothesis that araneoid sheet web weavers have 'escaped' from predatory wasps and that their radiation may be due in part to the evolution of 3-D web architectures. Unfortunately, the evolutionary significance of unique transitions, such as this, is difficult to test statistically (Guyer & Slowinski 1993).

CONCLUSIONS

The switch to three-dimensional web architecture obviously affected spider life histories in more ways than just predator avoidance, including changes in how spiders forage (e.g.

Janetos 1982). Defence against predatory wasps is unlikely to be the only factor that stimulated the radiation of the more than 6000 described species in the araneoid sheet web weavers, but we argue only that it was one factor, and, conceivably, one of the most important. Confounding variables such as size selection by wasps, the degree of diurnality of their spider prey, their detailed predatory behaviour, and more precise measurements of relative spider abundance could all be profitably studied to test this hypothesis further.

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SUPPLEMENTARY MATERIAL

The following material is available from <http://www.blackwellpublishing.com/products/journals/suppmat/ELE/ELE384/ELE384sm.htm>:

Appendix 1 Individual records of predation on spiders by all of the genera of spider hunting sphecid wasps for which data are available in the literature from 1900 to 2001.

Appendix 2 Individual faunal surveys of spiders used to estimate relative availabilities of wasp prey in the environment.

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