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Redesigning spider webs: Stickiness, capture area and the evolution of modern orb-webs

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ABSTRACT

An orb-web's ability to capture insects is enhanced by both increased capture area and increased stickiness per capture area. As spider size limits the amount of material that an orb-weaver can invest in the sticky prey capture threads of its web, these two strategies are in conflict. The origin of modern orb-weaving spiders of the large superfamily Araneoidea was associated with the origin of adhesive capture threads. These threads achieve their stickiness at a greater material economy than do the primitive cribellar capture threads found in orb-webs produced by the superfamily Deinopoidea. Consequently, araneoid orb-weavers have a greater amount of stickiness at their disposal. A comparison of orb-webs produced by these sister clades shows that araneoids expend this stickiness in a manner consistent with the hypothesis that increased stickiness per capture area is favoured over increased capture area. Araneoid orb-webs have, relative to spider weight, smaller capture areas than deinopoid orb-webs and, relative to web capture area, greater total stickinesses than deinopoid orb-webs. The stickiness per capture area of araneoid orb-webs is greater than that of deinopoid orb-webs and the spacing of capture thread spirals in araneoid orb-webs is equal to or less than that in deinopoid orb-webs. Thus, araneoid orb-webs are better equipped than deinopoid orb-webs to retain insects that strike the web. This increases the ability of araneoid spiders to subdue ensnared insects before they escape from the web and may favour the capture of larger prey.

Keywords: adhesive thread, Araneidae, capture thread, cribellar thread, orb-web, thread stickiness, Tetragnathidae, Uloboridae.

INTRODUCTION

Over 4200 species of spiders use orb-webs to capture flying insects. These species belong to the Orbiculariae clade, which is comprised of the sister superfamilies Deinopoidea and Araneoidea. The success of the aerial snares constructed by these spiders depends on the availability of insects and the web's ability to intercept and retain them. Insect availability is determined by the habitat in which a web is placed (Reichert and Cady, 1983; Wise and Barata, 1983; Craig, 1988, 1990). The web's ability to intercept these insects is influenced by its area (Eberhard, 1986), its orientation (Eberhard, 1989), its invisibility or attractiveness to insects (Craig, 1988, 1990; Craig and Bernard, 1990; Craig *et al.*, 1994), and by the

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visibility of a spider positioned at the web's hub (Craig and Freeman, 1991; Craig and Ebert, 1994). After encountering an insect, a successful orb-web must first absorb the force of this prey impact and then retain the struggling insect until a spider can subdue it (Chacón and Eberhard, 1980; Craig, 1987a,b). A web's architecture, strength and extensibility equip it to absorb and dissipate the force of a prey strike (Denny, 1976; Eberhard, 1986, 1989; Craig, 1987a,b; Lin *et al.*, 1995), and its sticky, spirally arrayed capture thread equips it to retain prey (Chacón and Eberhard, 1980; Eberhard, 1989; Opell, 1990, 1994a).

Capture thread plays a critical role in the operation of an orb-web as it forms the mesh that both intercepts and retains insects (Eberhard, 1986; Craig, 1987b; Opell, 1996). Capture thread is also considered to be the most energetically and behaviourally costly component of an orb-web (Sherman, 1994). The amount of material that orb-weavers of both the superfamilies Deinopoidea and Araneoidea can allocate to the production of capture thread is much more limited than the amount of silk that they can devote to the web's non-sticky supporting threads (Peters, 1937; Koenig, 1951; Witt *et al.*, 1968; Eberhard, 1972, 1986). This limit appears to be set by spider size. For spiders that construct new orb-webs each night, spider weight is directly related to web area (Opell, 1996), the total volume of material invested in a web's capture thread and the total stickiness of the web (Opell, 1997). These relationships support Eberhard's (1989, 1990) conclusion that there are trade-offs between the capture area of a web and the stickiness per square centimetre of its capture area. That is, a spider of a given size can maximize either capture area or stickiness per area, but it cannot construct a web with both a large capture area and a high stickiness per area.

Several factors suggest that the maintenance or increase of an orb-web's stickiness per capture area (SPA) should be favoured over an increase in its capture area. If the capture area of an orb-web increases and its SPA decreases, larger insects that are generally more profitable prey (Krebs and Davies, 1978) will more easily escape from the web because they are held less securely by its capture threads. Increased web area also increases the average distance a spider must travel to reach ensnared insects. This increases a spider's response time and affords a greater opportunity for insects of all sizes to struggle free of the web (Eberhard, 1989). A test of the hypothesis that increased SPA is favoured over increased web area requires a demonstrable increase in the total capture thread stickiness that is available to a lineage of orb-weaving spiders. Only then can it be determined if this additional resource is invested in a manner consistent with the hypothesis that SPA is favoured.

A major event in the evolution of orb-weaving spiders that occurred in the early Cretaceous (Selden, 1989) provides a unique opportunity to test this hypothesis. At this time, modern orb-weaving spiders of the superfamily Araneoidea diverged from primitive orb-weaving spiders of the superfamily Deinopoidea (Coddington, 1986, 1990a,b; Coddington and Levi, 1991). Members of the Deinopoidea produce dry, fuzzy cribellar capture thread that is supported by a pair of axial fibres and has an outer surface that is formed of thousands of fine, looped fibrils (Fig. 1a; Peters, 1983, 1984, 1986, 1992; Eberhard, 1988; Opell, 1990, 1993, 1994b,c, 1995, 1996; Eberhard and Pereira, 1993). This capture thread achieves its stickiness at a lower material economy than the viscous, adhesive capture threads that are produced by members of the larger Araneoidea clade (Opell, 1998). These adhesive capture threads are formed of a complex chemical solution that is deposited on the axial fibres as they issue from spigots on a spider's spinnerets (Vollrath *et al.*, 1990; Townley *et al.*, 1991; Vollrath and Tillinghast, 1991; Tillinghast *et al.*, 1993). This solution quickly coalesces into a series of regularly spaced viscous droplets (Fig. 1b) that owe their stickiness to glycoprotein nodules that lie within (Vollrath *et al.*, 1990; Vollrath and Tillinghast, 1991; Tillinghast *et al.*, 1993; Peters, 1995).

Consequently, members of both orb-weaving clades invest similar volumes of material in the capture threads of their webs, but araneoid orb-webs achieve a greater total stickiness than do orb-webs constructed by deinopoids of similar weights (Opell, 1997). By determining how this additional stickiness is deployed by araneoids, it is possible to test the hypothesis that increased SPA is favoured over increased capture area. This hypothesis makes four predictions. First, relative to spider weight, the capture areas of araneoid orb-webs should be equal to or less than those of deinopoid orb-weavers. If this is not the case, then greater SPA cannot be achieved by araneoids. Second, relative to the capture areas of their orb-webs, the total stickiness of araneoid orb-webs should exceed the total stickiness of deinopoid orb-webs. The greater the slope of this relationship, the greater the web's SPA. Third, the spacing of capture thread spirals in araneoid orb-webs should be equal to or less than that in deinopoid orb-webs. Unless this condition is met, the greater stickiness of araneoid capture threads would be spread over a larger web area and greater SPA could not be achieved. Fourth, araneoid orb-webs should have greater SPA indices than deinopoid orb-webs. The first two predictions are supported by phylogenetic analyses and the latter two by more traditional statistical tests. These results show how the economy of producing capture thread has influenced the design of spider webs and contributed to the success of araneoid orb-weavers that now constitute 95% of all orb-weaving spiders.

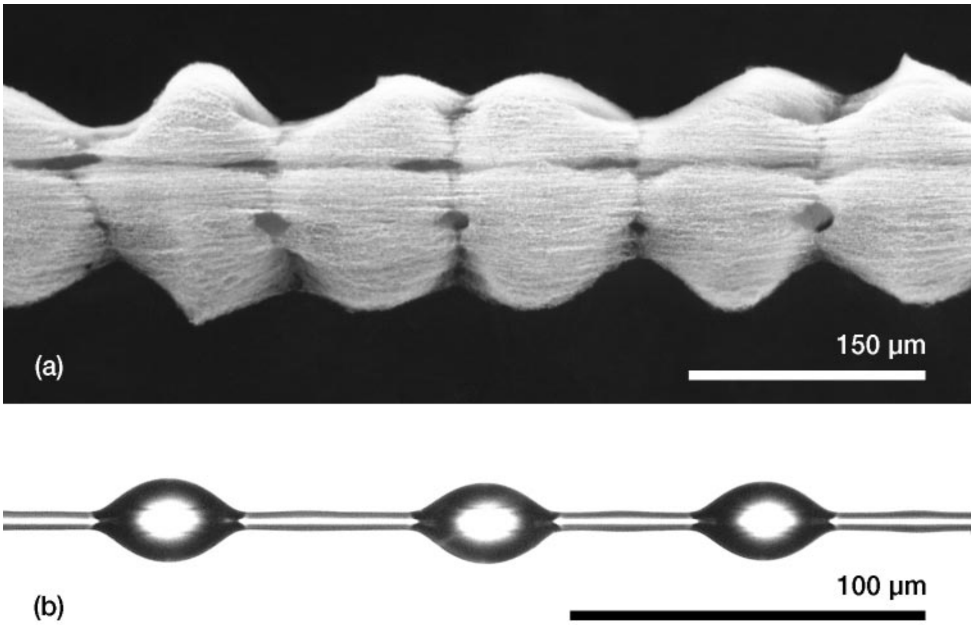

Fig. 1. Two types of capture threads found in orb-webs: (a) cribellar thread of *Hyptiotes cavatus* (scanning electron micrograph); (b) adhesive thread of *Argiope trifasciata* (light micrograph).

METHODS AND MATERIALS

Species studied

I compared the features of orb-webs constructed by adult females of nine species: four representing the deinopoid orb-web family Uloboridae, four representing the araneoid orb-web family Araneidae, and one representing the araneoid orb-web family Tetragnathidae. Species of Uloboridae and Araneidae were selected to represent the major clades of these families, as described by Coddington (1990b) and Scharff and Coddington (1997), respectively. The phylogenetic analysis described below also included two uloborid species of the genus *Hyptiotes*. The triangle-webs of these species are simpler than the orb-webs from which they are derived (Opell, 1979, 1982; Lubin, 1986), but, as their values are known (Opell, 1996), they are included to increase the resolution with which the ancestral values of orb-weaving species are determined. Figure 2 gives the relationship of these 11 species.

Web features

All of the species included in this study, with the possible exception of *Octonoba sinensis* (Opell, 1996), replace their webs daily; thus, the features of their webs can be compared. The length and stickiness of capture threads are taken from Opell (1996, 1997). Since web features vary intraspecifically (Eberhard, 1990; Sherman, 1994), the mean values of webs produced by 18–41 individuals per species were used in this study. I computed the capture area of an orb-web as the difference between the area inscribed by its outermost and its innermost capture spiral turns, thereby excluding the web's central free zone where no capture thread is found. The capture areas of triangle-webs were measured as the area inscribed by the web's inner- and outermost capture spirals and its upper and lower frame lines. As described more fully by Opell (1996, 1997), these measurements and those of

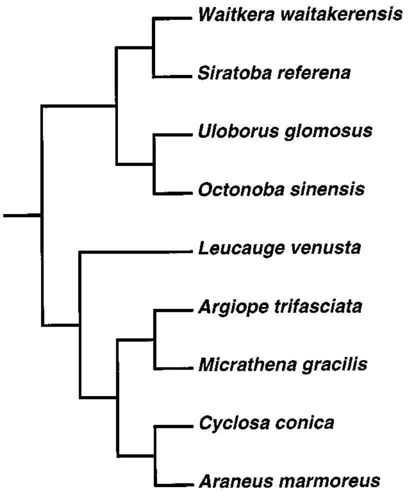

Fig. 2. Phylogeny of species in this study (based on Coddington, 1990b; Scharff and Coddington, 1997).

cribellar capture thread lengths were made with a digitizing table from enlarged photographic prints of webs that were dusted with corn starch to make their threads more visible (Carico, 1977). After photographing a web, the spider that constructed it was collected and weighed.

I determined the spiral spacing of orb-webs by first measuring the distance between the inner- and outermost capture spiral turns of four radii that diverged at 90° angles. In vertical araneoid orb-webs, this included one radius from above and one radius from below the web's hub to account for the asymmetry that is often found in these webs (Nentwig, 1985). The total measured distance of these four radii was then divided by the total number of inter-spiral spaces to determine mean spiral spacing. Triangle-webs constructed by *Hyptiotes* species are formed of four diverging radii that inscribe three capture sectors. I determined the spiral spacing of these webs by first measuring the distance between the inner- and outermost capture spiral along the radius that formed the top of each web sector. The total of these distances was divided by the total number of inter-spiral spaces to determine mean spiral spacing.

Phylogenetic analysis

Two methods have been developed for examining the relationships among features in a phylogenetic context: the independent contrast method of Felsenstein (1985), as implemented by programs such as the Compare program of Martins (1995) and the Comparative Analysis of Independent Contrasts program of Purvis and Rambaut (1995), and the ancestor-reconstruction method of Huey and Bennett (1986, 1987). Both methods minimize the influence of phylogenetic relationship as they analyse directional changes in continuous characters. The independent contrast method does so by computing differences between the features of sister taxa (both extant taxa and their inferred ancestors), whereas the ancestor-reconstruction method calculates the changes in features from their inferred ancestral states to the states expressed by extant taxa (see Harvey and Pagel, 1991, for a review of these approaches).

I chose the ancestor-reconstruction method for this study because data for only four cribellate orb-weaving species are available. This method produces a set of changes for each species, whereas the independent contrast method produces one fewer set of contrasts than the number of terminal taxa. Therefore, only the ancestor-reconstruction method allows features of deinopoid and araneoid orb-webs to be compared. I determined the ancestral values of each species' weight and web area using the rooted, minimized sum of squared changes option in the continuous character tracing section of the MacClade 3.02 phylogenetic program (Maddison and Maddison, 1992). I then calculated the changes from these inferred ancestral states to those expressed by each of the nine orb-weaving species and examined the relationships between these changes with regression statistics.

RESULTS

Web area

Table 1 presents data used in this and the following analyses. A Shapiro-Wilk *W*-statistic showed that change in spider weight was normally distributed for all orb-weavers ($P = 0.44$),

Table 1. The weights and web features of uloborid (from Opell, 1996) and araneoid species (mean ± 1 standard error; inferred ancestral values are given in square brackets)

Species (sample size)	Spider weight (mg)	Capture thread length (cm)	Capture thread stickiness (μN · mm^{-1})	Total web stickiness (mN)	Total web capture area (cm^{2})	Stickiness per capture area (μN·cm^{-2})	Capture spiral spacing (mm)
Uloboridae							
1. *Waitkera waitakerensis* ($n = 27$)	7.8 ± 0.3 [15.7]	329 ± 28	15.45 ± 0.82	51 ± 4 [62]	92 ± 9 [109]	596 ± 26	3.6 ± 0.1 [3.4]
2. *Siratoba referena* ($n = 23$)	4.1 ± 0.2 [15.7]	242 ± 25	11.46 ± 0.80	28 ± 3 [62]	65 ± 9 [109]	531 ± 22	2.5 ± 0.1 [3.4]
3. *Hyptiotes gertschi* ($n = 41$)	8.2 ± 0.2 [12.1]	146 ± 7	29.84 ± 2.17	44 ± 2 [58]	96 ± 6 [118]	483 ± 14	8.5 ± 0.3 [6.1]
4. *Hyptiotes cavatus* ($n = 27$)	8.1 ± 0.6 [12.1]	169 ± 8	26.18 ± 1.70	44 ± 2 [58]	72 ± 5 [118]	640 ± 19	4.6 ± 0.2 [6.1]
5. *Uloborus glomosus* ($n = 27$)	6.8 ± 0.3 [13.0]	392 ± 27	15.38 ± 1.02	60 ± 4 [96]	204 ± 12 [272]	310 ± 18	5.7 ± 0.3 [5.5]
6. *Octonoba sinensis* ($n = 24$)	12.2 ± 0.8 [13.0]	821 ± 46	17.02 ± 1.19	140 ± 8 [96]	426 ± 32 [272]	346 ± 14	5.5 ± 0.2 [5.5]
Araneidae							
7. *Argiope trifasciata* ($n = 25$)	474.0 ± 51.6 [260.2]	2321 ± 173	27.15 ± 1.99	630 ± 47 [480]	848 ± 74 [470]	778 ± 39	3.9 ± 0.2 [2.6]
8. *Araneus marmoreus* ($n = 15$)	677.1 ± 75.0 [302.8]	2204 ± 139	34.76 ± 4.21	766 ± 48 [407]	600 ± 42 [351]	1307 ± 76	3.1 ± 0.2 [2.4]
9. *Cyclosa conica* ($n = 23$)	8.9 ± 0.8 [302.8]	692 ± 55	11.47 ± 1.03	79 ± 6 [407]	92 ± 7 [351]	855 ± 37	1.6 ± 0.1 [2.4]
10. *Micrathena gracilis* ($n = 21$)	84.3 ± 5.0 [260.2]	1529 ± 81	28.34 ± 3.12	433 ± 23 [480]	201 ± 12 [470]	2333 ± 75	1.3 ± 0.0 [2.6]
Tetragnathidae							
11. *Leucauge venusta* ($n = 18$)	20.6 ± 1.7 [104.2]	859 ± 69	20.01 ± 2.50	172 ± 14 [241]	209 ± 18 [262]	894 ± 54	2.4 ± 0.2 [2.8]

for deinopoid orb-weavers ($P = 0.89$) and for araneoid orb-weavers ($P = 0.63$). For both clades, $\log_n$ transformation improved the normality of change in web area (for all orb-weavers, $W = 0.93$–0.94, $P = 0.51$–0.55; for deinopoids, $W = 0.81$–0.91, $P = 0.12$–0.49; for araneoids, $W = 0.88$–0.91, $P = 0.31$–0.49). Therefore, I used change in $\log_n$ web area for comparisons of deinopoid and araneoid orb-webs.

In both deinopoids and araneoids, change in $\log_n$ web capture area was directly and significantly ($P \leq 0.05$) related to change in spider weight (Fig. 3). A test of the homogeneity of these regression slopes showed that they differ ($F = 6.74$, $P = 0.049$), with the slope of the regression line for deinopoid orb-weavers being greater than that for araneoid orb-weavers. Thus, relative to spider weight, the orb-webs of araneoids have a smaller capture area than those of deinopoids.

Web stickiness

Change in total web stickiness was normally distributed for both deinopoid and araneoid orb-weavers ($P = 0.16$ and 0.92, respectively) and for both clades was directly related to change in $\log_n$ web capture area (Fig. 4). A test of the homogeneity of these regression slopes showed that they did not differ ($F = 1.66$, $P = 0.254$). The negative result of this test in the face of the good fit of both regression lines is explained by the fact that the values of deinopoid orb-weavers have very little spread and that three of the four points fall very near the regression line for araneoid orb-weavers. A *t*-test of the slopes of these two regressions ignores these interactions and treats each regression independently. It shows that their

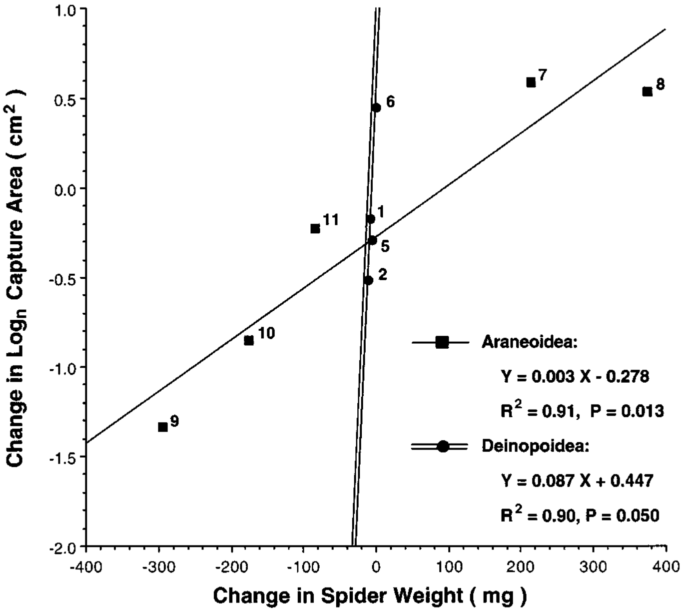

Fig. 3. Regression of change in spider weight and change in $\log_n$ web capture area for deinopoid and araneoid orb-weaving spiders. Numbers are species numbers from Table 1.

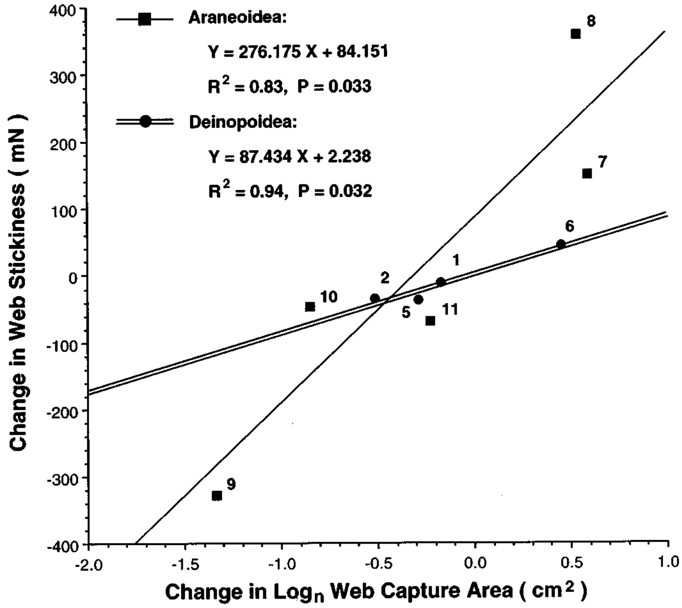

Fig. 4. Regression of change in web capture area and change in total web stickiness for deinopoid and araneoid orb-weaving spiders. Numbers are species numbers from Table 1.

slopes do, in fact, differ ($t = 2.974$, $P = 0.032$) and documents that, relative to web capture area, araneoid orb-webs are stickier than deinopoid orb-webs.

Spiral spacing

Change in spiral spacing was normally distributed for araneoid orb-weavers ($P = 0.71$), but not for deinopoid orb-weavers ($P = 0.042$). Transformations failed to normalize spiral spacing. However, for neither clade was there a relationship between change in spiral spacing and change in spider weight (deinopoids, $F = 1.18$, $P = 0.391$; araneoids, $F = 9.32$, $P = 0.055$).

Spiral spacing differed among species and tended to be greatest in orb-webs constructed by deinopoids and smallest in orb-webs constructed by araneoids (Fig. 5). Spiral spacing was not normally distributed in four species ($P < 0.05$), but became normal when $\log_n$-transformed ($P > 0.08$). A one-way analysis of variance showed that $\log_n$ spiral spacing differed among the 11 species in this study ($n = 279$, $F = 178.85$, $P = 0.0001$). A Ryan *Q*-test (alpha = 0.05) showed that the two orb-webs with the greatest spiral spacing are produced by deinopoid species and the two orb-webs with the smallest spiral spacing are produced by araneoid species (Fig. 5). Both the next greatest and the next smallest spiral spacing were found in orb-webs produced by pairs of species consisting of one deinopoid and one araneoid species. For both deinopoids and araneoids, mean species' spiral spacing was normally distributed ($P > 0.77$). A *t*-test comparing these species' means shows that the value of araneoid species (2.5 mm) was less than that for uloborid species (5.1 mm; $t = 2.54$, $P = 0.03$).

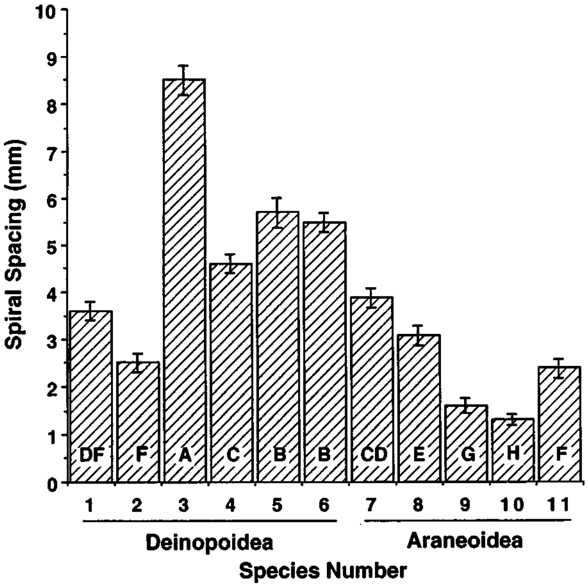

Fig. 5. Comparison of the capture spiral spacing of deinopoid and araneoid orb-webs. Numbers refer to species numbers in Table 1. Error bars denote ±1 standard error. Letters refer to similar mean values as determined by a Ryan Q-test with an alpha of 0.05.

Stickiness per web area

For both deinopoids and araneoids, change in SPA was normally distributed ($P = 0.59$ and 0.869, respectively). However, for neither clade was change in SPA related to change in spider weight ($F = 0.02$, $P = 0.908$ and $F = 0.16$, $P = 0.715$, respectively).

A comparison of the mean SPAs of webs constructed by the 11 species studied (Fig. 6) also showed that araneoid orb-webs are stickier than deinopoid orb-webs. The SPA of two araneoid species was not normally distributed ($P < 0.05$), but for all species $\log_n$ SPA was normally distributed ($P > 0.09$). A one-way analysis of variance showed that $\log_n$ SPA differed among the 11 species in this study ($n = 301$, $F = 163.86$, $P = 0.0001$). A Ryan Q-test (alpha = 0.05; Day and Quinn, 1989) showed that the $\log_n$ SPAs of all araneoids ranked above those of all uloborids (Fig. 6). Among araneoid species, mean species SPA was not normally distributed ($P = 0.05$), but for both araneoid and deinopoid species, $\log_n$ mean species SPA was normally distributed ($P > 0.17$). A t-test showed that the mean SPA of araneoid species (1233 $\mu\text{N}\cdot\text{cm}^{-2}$, $\log_n = 7.03$) was greater than that of deinopoid orb-weaving species (488 $\mu\text{N}\cdot\text{cm}^{-2}$, $\log_n = 6.15$) ($t = 3.89$, $P = 0.004$).

DISCUSSION

The results of this study support the hypothesis that increased SPA is favoured over increased capture area and show that the origin of modern adhesive orb-weavers was marked by an increase in SPA and not by an increase in capture area. Not only do

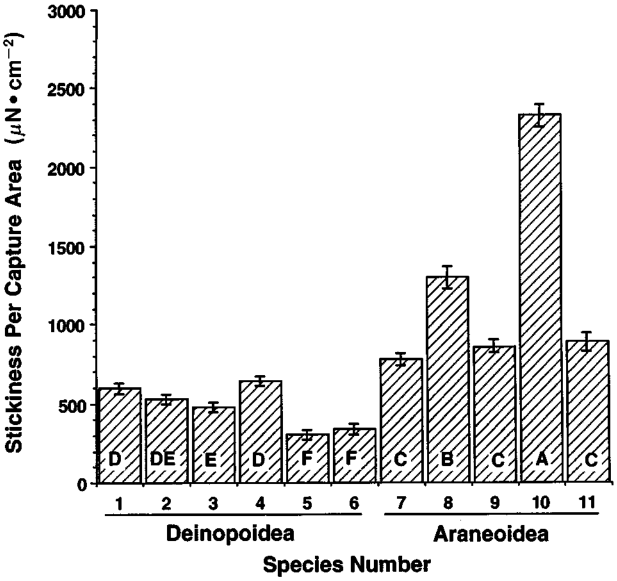

Fig. 6. Comparison of the stickiness per capture area of deinopoid and araneoid orb-webs. Numbers refer to species numbers in Table 1. Error bars denote ±1 standard error. Letters refer to similar mean values as determined by a Ryan *Q*-test with an alpha of 0.05.

araneoid orb-webs contain greater total stickinesses than deinopoid orb-webs (Opell, 1997), but, relative to spider weight, these webs are smaller than deinopoid orb-webs and contain capture spirals whose spacing is equal to or less than that of deinopoid orb-webs. Each of these factors contributes to the greater SPA that characterizes araneoid orb-webs.

Differences between deinopoid and araneoid orb-webs show that changes in web features that increase prey retention over prey interception have been favoured. A study of prey capture by artificial spider webs demonstrates the potential for this increased stickiness to enhance an orb-web's ability to capture prey (Chacón and Eberhard, 1980). When the stickiness of these networks was doubled, they retained 38% more insects. These values may not be directly applicable to the performance of real orb-webs, but they document the contribution that increased stickiness makes to increased prey capture. However, web stickiness is not the only factor that enhances a spider's ability to capture prey. Factors such as the speed with which a spider runs to an ensnared insect and the spider's adeptness at subduing the insect also contribute to prey capture success (Eberhard, 1989).

The orb-webs of both the Deinopoidea and the Araneoidea show considerable interspecific variability in spiral spacing and SPA that cannot be explained by differences in spider weight. Although orb-webs do not act as simple sieves (Nentwig, 1983; Eberhard, 1986, 1990; Craig, 1987b) and orb-weaving spiders appear to be rather generalized predators (Eberhard, 1990), spiral spacing is thought to contribute to prey specialization (Buskirk, 1975; Robinson and Robinson, 1978; Uetz *et al.*, 1978; Wise and Barata, 1983;

Higgins, 1987). Spiral spacing does influence the type of insects that a web can most effectively capture (Eberhard, 1986, 1990). Thus, interspecific differences in spiral spacing and SPA may favour the capture of insects of a particular size or flight characteristic.

The greater stickiness per capture area of araneoid orb-webs is not the only factor that appears to have contributed to the success of this clade. The adhesive orb-webs of araneoids differ from the cribellate orb-webs of uloborids in their thread composition, orientation, visual properties and in the extensibility of their capture threads. The transition from cribellar to adhesive capture threads was associated with a shift from horizontal to vertical orb-web orientation (Bond and Opell, 1998), which experimental studies show increases the rate of prey interception. Vertically oriented orb-web models capture more insects and retain them for longer periods of time than do horizontally oriented models with the same capture thread stickiness (Chacón and Eberhard, 1980). When the orientation of actual araneoid orb-webs was changed, vertically oriented webs retained prey longer than horizontally oriented webs (Eberhard, 1989). Additionally, insects that struggled free of vertical webs were 19 times more likely to be recaptured by the web's other threads than those that struggled free of horizontal webs (Eberhard, 1989).

Most adhesive capture threads also reflect less ultraviolet light than cribellar threads (Craig and Bernard, 1990; Craig *et al.*, 1994) and are, therefore, less visible to insects in certain habitats (Craig, 1988, 1990). Differences at the molecular level, although poorly understood, contribute to these and other differences in the properties of araneoid and deinopoid threads (Craig, 1992). This shift in the spectral properties of araneoids tends to increase prey capture and allow araneoids to occupy more brightly lighted habitats (Craig *et al.*, 1994). Adhesive capture threads are also more extensible than cribellar threads (Köhler and Vollrath, 1995) because each of their viscous droplets serves as a miniature, self-tensing windlass mechanism (Vollrath and Edmonds, 1989). This helps maintain the tension of capture threads under windy conditions and may contribute to overall web extensibility (Craig, 1987b) and, therefore, better equip a web to absorb the force of prey strikes through aerodynamic dampening (Lin *et al.*, 1995).

A comparison of the functional properties of orb-webs constructed by the Deinopoidea and Araneoidea provides insights into the performance of orb-webs and the differences between webs constructed by members of these sister clades. However, considering these webs as simply inferior and superior versions of the same type of aerial snare may be a fallacy comparable to considering amphibians and reptiles as inferior versions of birds and mammals. Differences in the orientation of cribellar and adhesive orb-webs (Bond and Opell, 1998) and in the microhabitats where these webs are placed (Craig *et al.*, 1994) suggest that the design of adhesive orb-webs adapts them to meet a different set of demands than those imposed on cribellate orb-webs and probably also to capture a different guild of insects. Thus, as Craig *et al.* (1994) and Bond and Opell (1998) have proposed, the success of araneoid orb-weavers may be attributed not principally to their ability to outcompete deinopoid orb-weavers, but rather to their ability to occupy new adaptive zones not available to deinopoids.

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