

Tenacity and silk investment of two orb weavers: considerations about diversification of the Araneoidea

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Abstract. Orbiculariae consists of two major clades: the cribellate Deinopoidea and the much more diverse ecribellate Araneoidea. It has been hypothesized that the higher diversity of Araneoidea is a consequence of the superiority of the viscid orb web. However, this explanation seems incomplete; for example, cribellate silk may perform better than viscid silk in some contexts. Here, we consider the hypothesis that the diversification of Araneoidea was facilitated by changes in microhabitat occupation behavior due to the cheaper viscid orb web. In the present work we investigate the idea that the reduction in site tenacity caused by the emergence of the viscid orb web has led to an increase in the exploration of different resources and to a greater diversification of the Araneoidea through the evolutionary time. To test this idea, we evaluated the response of one cribellate orb web spider (*Zosis geniculata* Olivier 1789, Uloboridae) and one ecribellate orb web spider (*Metazygia rogenhoferi* Keyserling 1878, Araneidae) to abrupt prey absence. The changes in site tenacity and the day-to-day investment in web silk were evaluated. Spiders with three-dimensional webs tend to exhibit greater site tenacity than spiders making orb webs. *Zosis geniculata* and *M. rogenhoferi* show similar site tenacity when prey is ample. When prey is unavailable, the tenacity of the cribellate species increases while the tenacity of the ecribellate remains unchanged, and the silk investment of both species decreases. However, this decrease in silk investment is more extensive in *Z. geniculata*. These results coincide with the idea that a less costly ecribellate orb web leads to a lower tenacity and suggest that more frequent microhabitat abandonment in a context of insect radiation (Neoptera) leads to more diverse and opportunistic exploration of microhabitats that, in the long term, may be one explanation for the greater Araneoidea diversification.

Keywords: cribellate, evolution, Araneidae, Uloboridae, spiders

Resumo. Orbiculariae é composto por dois grandes clados de aranhas, as cribeladas Deinopoidea e as não cribeladas e muito mais diversas Araneoidea. A hipótese mais aceita é a de que a maior diversificação do grupo ecribelado (Araneoidea) é devido à superioridade da teia orbicular viscosa. Porém, essa explicação não é suficiente para explicar a diversificação de Araneoidea já que o fio cribelado, por exemplo, pode ser mais eficiente em alguns contextos ecológicos. Assim, consideramos a hipótese de que a diversificação de Araneoidea foi facilitado pela redução na tenacidade pelo microlocal, consequência do surgimento de uma teia de fio viscoso mais barato. Para começar a explorar essa idéia nós avaliamos a resposta de uma espécie cribelada (*Zosis geniculata* Olivier 1789, Uloboridae) e de uma ecribelada (*Metazygia rogenhoferi* Keyserling 1878, Araneidae) a um evento de indisponibilidade de presas. Acompanhamos as mudanças na tenacidade e no investimento em seda dia-a-dia. As aranhas construtoras de teias caras tendem a apresentar maior tenacidade pelo microlocal do que as construtoras de teias baratas. Orbitelas cribeladas e ecribeladas também apresentam diferentes investimentos na construção e manutenção da teia. Com a ingestão regular de presas *Z. geniculata* e *M. rogenhoferi* apresentam tenacidades similares. Quando cessa a oferta de presas, a tenacidade da espécie cribelada aumenta enquanto a espécie ecribelada mantém-se inalterada, porém, o investimento em seda de ambas diminui, e *Z. geniculata* reduz mais intensamente o investimento em seda. A maior frequência no abandono da teia teria permitido, de modo oportunístico, uma maior e mais rápida exploração de recursos novos advindos da radiação do grupo de insetos alados modernos. O efeito dessa maior mobilidade pelo ambiente, ao longo do tempo evolutivo, poderia ajudar a explicar a radiação de Araneoidea em relação a seu grupo-irmão cribelado.

Palavras-chave: cribeladas, evolução, Araneidae, Uloboridae, aranhas

Current hypotheses about the extreme diversification of araneoid orb weavers investigate synapomorphies of the group as putative key adaptations. Web features such as orb verticality (Eberhard 1989; Opell et al. 2006) or the presence of viscid silk (Bond & Opell 1998) have been suggested as possible innovations causally related to species diversification. Better adhesiveness and extensibility (Köhler & Vollrath 1995), lower cost (Opell 1996, 1998), or low UV reflectance (Craig et al. 1994) have all been investigated as features that potentially have enhanced the fitness of viscid orb weavers as opposed to the primitively cribellate deinopoids. Nevertheless, these hypotheses are vague in suggesting how this specific improvement in performance affects fitness since they did not discuss the context by which they are proposed to increase

fitness. Some cribellate orb weavers, for example, also spin vertical webs (Lubin 1986); viscid threads are not necessarily more adhesive (Opell 1996, 1998) or extensible (Opell & Bond 2000; Blackledge & Hayashi 2006) than cribellate silk; high UV reflectance can also enhance fitness by attracting insects (Craig & Ebert 1994; Watanabe 1999; Li et al. 2004) or being a defense against predators (Craig & Freeman 1991; Zschokke 2002; Bruce et al. 2005). In this paper, we offer a previously unexplored hypothesis: changes in site tenacity could have contributed to Araneoidea radiation.

Vollrath & Selden (2007) suggest that orb web spider evolution might be a predator-prey arms race concurrent with the rise of the modern flying insects (pterygote Neoptera). In this evolutionary scenario, cribellate and viscid orbweavers

began with different potentials to take advantage of the new resources where a less costly and more quickly built web, along with the lower tenacity, might have given viscid orbweavers a competitive edge. Even in current orb web spiders, we can find indications of this ancient behavioral flexibility. Some orb weavers are not restricted to web site choice rules (Eberhard 1971). Thus we should expect a reduction in site tenacity to be associated with a more widespread occupation of the habitat. Reduced site tenacity should result in the occupation of a larger range of microhabitats, leading to more opportunities for speciation. We propose that the more diverse clade of ecribellate orb weavers will have lower site tenacity in relation to the less diverse clade of cribellate orb weavers.

Site tenacity varies in response to ecological conditions. Desert spiders present higher tenacity, either from being subjected to a high physiological stress, or because of a relatively high risk of not reaching a new suitable site (Riechert & Gillespie 1986; Henschel & Lubin 1997). Web damage raises the chances of site abandonment (Gillespie & Caraco 1987), and abandonment occurs earlier from webs with a high production cost (Eberhard 1971) than on low cost webs (Craig 1989). In general, high cost of the sheet webs compared to the orb webs is also associated with a higher tenacity (Janetos 1986; Riechert & Gillespie 1986).

The association of changes in web costs with changes in site tenacity shows that ecological factors are not solely responsible for site abandonment. General evolutionary changes in web building and architecture (web costs) could be associated with general phylogenetic patterns of site tenacity. Several indirect evidences point to an evolutionary change from a high cost orb web among cribellate deinopoids (Uloboridae plus Deinopidae) to a low cost orb web in the remaining Orbiculariae clade. The duration of a web building bout ranges from 3 to 5 h among the cribellate orb weavers to about 30 min among the ecribellate araneids (Lubin 1986; Zschokke & Vollrath 1995a,b). The energy consumption must be higher among uloborids since the building of the cribellate adhesive spiral requires intense and repetitive combing movements of legs IV (Eberhard 1988), an unnecessary behavior among ecribellate orb weavers (Peakall & Witt 1976). The cribellate silk is highly proteic, much more so than the 80% water volume viscous droplets from the ecribellate orb weavers (Crews & Opell 2006). Finally, cribellate spiders recycle less of their silk than ecribellate ones (Lubin 1986; Opell 1998).

Here, we evaluate the hypothesis that the diversification of ecribellate orb weavers may in part result from an evolutionary reduction in site tenacity that could have led to a faster and more opportunistic exploitation of unpredictable resources, thus facilitating the diversification in the clade. As a first step in the evaluation of this new hypothesis, in this paper we test the idea that lowered costs in orb web building and maintenance are associated with lowered tenacity values. In order to explore this new hypothesis, we performed a preliminary survey to compare a cribellate and an ecribellate orb weaver species in relation to their site tenacity and silk investment.

METHODS

We chose *Zosis geniculata* Olivier 1789 (Uloboridae) and *Metazygia rogenhoferi* Keyserling 1878 (Araneidae) as

representatives of the cribellate and ecribellate orb weavers, respectively. The choice was based on several common factors of these species. Both species have similar adult body sizes, they spin similar size orb webs, they do not present marked seasonality, and their families are at the base of the sister clades Deinopoidea (cribellate) and Araneoidea (ecribellate). The specimens were collected in São Paulo city, and voucher specimens were deposited in the arachnological collection at Instituto Butantan (IB-88434 to IB-88452; *M. rogenhoferi* plus nematodes IB-88441, IB-88439, IB-88622; A.D. Brescovit, curator).

Adaptation to laboratory conditions.—We brought adult females to the laboratory and kept them in individual acrylic boxes (31 × 31 × 12 cm) in a room with inverted day-night cycle (12 h dark:12 h light) and low temperature (24° to 26° C) and humidity (76% to 81% RH) variation. After building their first webs, the spiders were marked with gouache ink and overfed with a diet of crickets (of the same size of the spiders, mean weight = 7.23 ± 0.50 mg, *n* = 10) three times a week for at least 20 days, until the spiders built webs regularly in the boxes. Many *Metazygia rogenhoferi* specimens died in the first week of feeding, due to nematode or fungal parasitism. After the first week in the laboratory, no more spiders died due to parasitism.

Experimental procedure.—After the spiders adapted to laboratory conditions, we separated 40 spiders (20 of each species) for the experiment. They each were fed one cricket before their acrylic boxes were opened so that they could now leave the original web building site. In this free condition, spiders were fed one cricket (of the same size as the spider) every four days. The food was repeated five times in succession (totaling 21 “Fed” days = F condition); subsequently feeding was abruptly interrupted for the rest of the experiment (the “Unfed” = U condition), which continued until all spiders had left the original web site. This change in diet was planned in order to induce site abandonment in the laboratory so that we could compare abandon times between the species under controlled conditions. Thus we measured the tenacity by the number of days from the opening of the acrylic box until the abandonment of the web for each spider. Also, we measured, for both treatments (F and U) and each spider species, the cumulative investment obtained through the sum of the length of all capture spiral reconstructions over each 21-day treatment period. Every day we also measured, for each reconstruction, the length of the adhesive spiral on the reconstruction (cm), the area reconstructed (cm²), the total area of the final web (old plus reconstructed portions), and the adhesive thread density in the reconstruction (cm/cm²). We used the mean of the successive webs from each individual spider in each 21-day treatment period to proceed with the analysis. We assumed that thread thickness and amount of glue were constant. This provided only an approximate estimate of investment since the amount of glue may often change (Crews & Opell 2006). Web measures were taken from digitized photographs with the aid of the freeware UTHSCSA Image Tool 3.0 (<http://ddsdx.uthscsa.edu/dig/itdesc.html>). Each reconstruction was identified by comparing radius and spirals at the hub with those immediately before web reconstruction pictures (Fig. 1).

Statistical analysis.—We used the Kaplan-Meier procedure (Motulsky 1995) to estimate, for each species, the probability

of remaining at the original web site (the acrylic box), as a function of the time since the beginning of the experiment (i.e., the tenacity function). In this analysis, individuals who died before leaving the original web site are considered censored data. A prerequisite of the Kaplan-Meier procedure is that the number of censored individuals is not correlated with the survival function itself, that is, that the death of the subjects is not correlated with the treatment. Although this prerequisite was certainly valid at the beginning of the unfed treatment, this was not so after a long period of starvation. In order to overcome this difficulty, we excluded from the comparison all tenacity measurements after a strong reduction in the size of the abdomen of the spiders (after 28 days of starvation). We expected the uloborid to have a higher probability of staying in the original web site, meaning a higher tenacity. The Breslow statistic (Motulsky 1995) was used to test for differences in tenacity between the two species. The Breslow test is more conservative than other similar tests (Log-Rank and Tarone-Ware), and also more appropriate, since the tenacity functions in our experiment do not vary proportionately to each other (Gross & Clark 1975). The differences in silk investment between treatments (F and U) were tested, for each species, with the t-test or Wilcoxon statistic. Differences in silk investment between species, either in the F or in the U condition, were tested through the paired t-test or

Mann-Whitney statistic (Fowler et al. 1998). Only spiders that did not abandon the acrylic boxes during the 21-day U treatment period were considered in the investment analyses. In order to render silk investment under the two conditions (F and U) comparable, we used only the data from the first 21 days in the Unfed condition (to equal the 21 days in the F condition). Statistical analyses were performed with the software packages SPSS 13.0 (Kaplan Meier and Breslow) and Statistica 7.0 (for silk investment). We considered $\alpha = 0.05$ as the critical level of significance for all statistical tests.

RESULTS

Web site tenacity.—While the araneid and the uloborid do not differ in the probability of leaving the web site under the fed condition (Breslow = 0.069; $P = 0.792$; $n = 40$) when unfed, the uloborid is more tenacious than the araneid (Breslow = 4.956; $P = 0.026$; $n = 27$). *Metazygia rogenhoferi* does not seem to alter its tenacity in response to hunger and the probability of leaving the web site declined almost steadily throughout the experimental period. *Zosis geniculata*, however, presented periods of maintenance and periods of abrupt decline in the probability of leaving the web site (Fig. 2). *Zosis geniculata* remained for longer starvation periods; the last *Z. geniculata* left the web site after 75 days without food, while the last *M. rogenhoferi* abandoned her web site after 57 days without food.

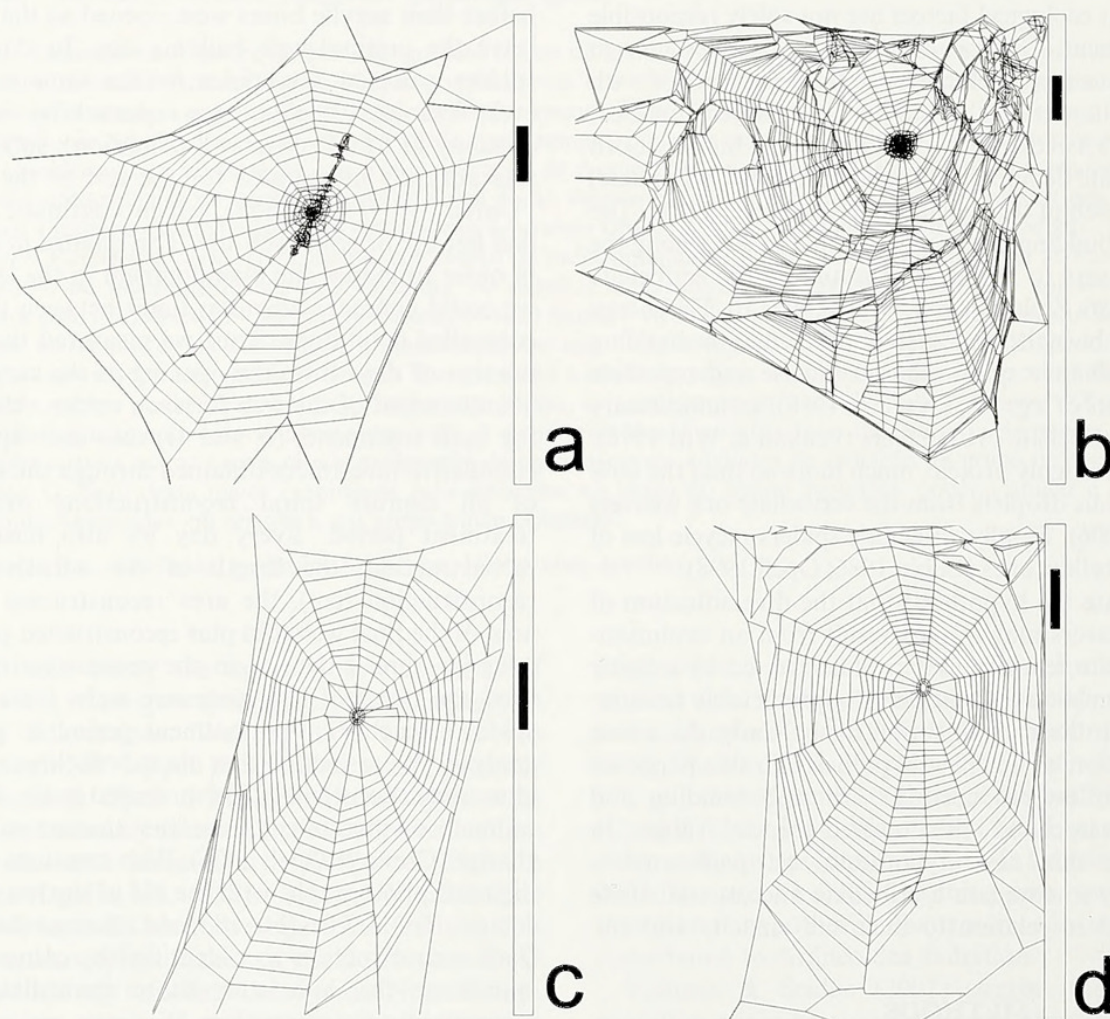


Figure 1.—Drawings based on photographs of webs, illustrating the first web of *Z. geniculata* (a) and *M. rogenhoferi* (c) and partial reconstructions (b and d, respectively).

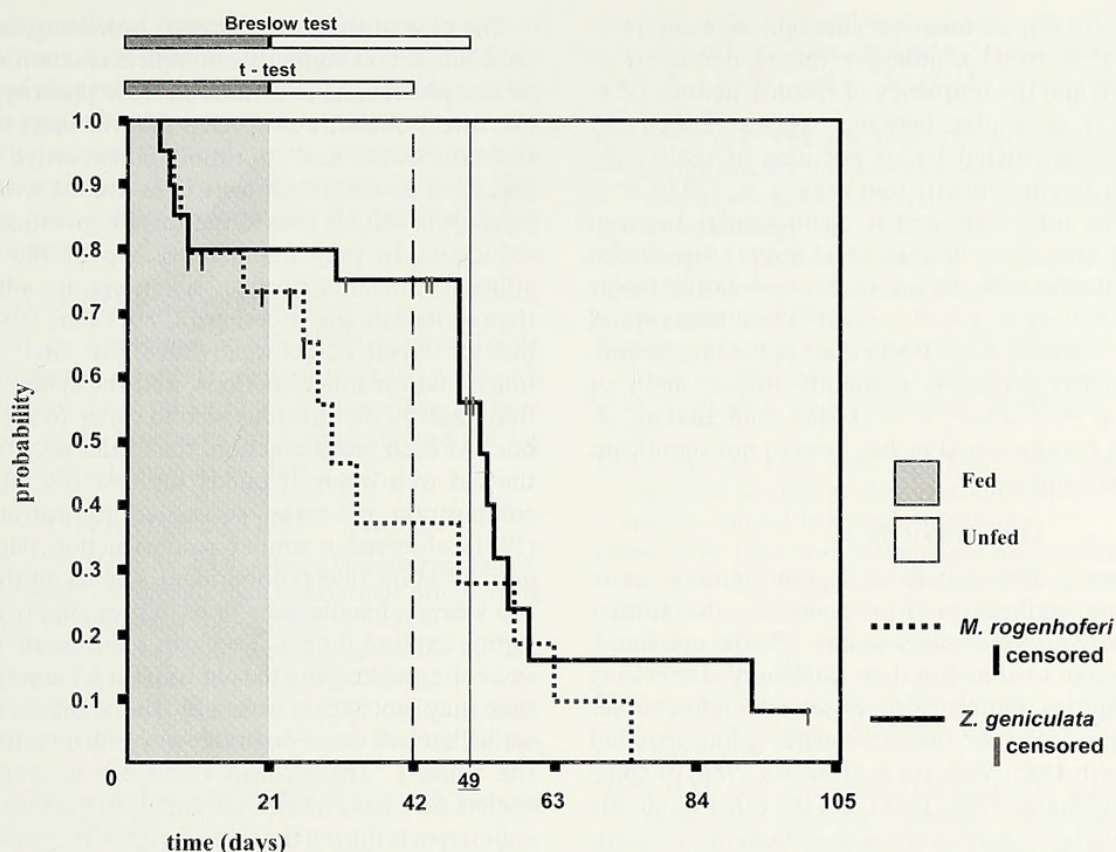


Figure 2.—Permanence probability curves obtained with the Kaplan-Meier Procedure from survival analysis statistics. Upper bars shows the periods used in the comparative statistical analysis.

Table 1.—Web measurements and reconstruction frequencies from *M. rogenhoferi* and *Z. geniculata* (mean and standard deviation) of individuals after 21 days on the Fed and the Unfed periods.

Species	Measurements	Fed		Unfed	
		Mean	SD	Mean	SD
<i>Metazygia rogenhoferi</i>	reconstruction frequency	8	2.99	6	1.26
	cumulative capture spiral length (cm)	5206.93	2584.64	3774.47	1535.07
	capture spiral length (cm/web)	718.92	143.81	655.47	112.24
	reconstructed area (cm ²)	272.64	66.77	315.51	79.34
	total web area (cm ²)	388.50	106.39	414.89	80.43
	threads density (cm/cm ²)	2.33	0.38	2.11	0.17
<i>Zosis geniculata</i>	reconstruction frequency	6	1.91	2	1.10
	cumulative capture spiral length (cm)	2278.17	1311.88	424.26	317.29
	capture spiral length (cm/web)	333.08	130.17	188.05	134.73
	reconstructed area (cm ²)	120.54	42.31	73.16	49.30
	total web area (cm ²)	304.30	112.13	445.54	137.89
	threads density (cm/cm ²)	2.77	0.61	2.89	0.82

Silk investment.—All the measurement results are summarized in Table 1 and correspond only to spiders that did not abandon the acrylic boxes in the 21-day U treatment period. The different feeding regimes do not alter the measured parameters of the web of *M. rogenhoferi* ($n = 4$ for all tests). Neither the linear cumulative silk investment ($t = 2.017$; $P = 0.137$) as in mean thread investment per web ($t = -0.100$; $P = 0.926$), nor the web reconstruction area ($t = -2.906$; $P = 0.062$), total web area ($t = -0.567$; $P = 0.610$), adhesive thread density ($t = 2.390$; $P = 0.097$), or the frequency of web reconstruction ($Z = 1.604$; $P = 0.109$) change with diet. In contrast, *Z. geniculata* ($n = 14$ for all tests) reduced silk

investment, diminishing the linear adhesive thread cumulative investment ($t = 5.806$; $P < 0.001$) as in mean thread investment per web ($t = 2.808$; $P = 0.015$), web reconstruction area ($t = 2.794$; $P = 0.015$), total area ($t = -6.580$; $P < 0.001$), and the frequency of web reconstruction ($Z = 3.296$; $P = 0.001$) without altering adhesive thread density ($t = -0.575$; $P = 0.575$).

Species differ in most web parameters ($n = 18$ for all tests). Fed *M. rogenhoferi* reconstructed larger portions of their webs (reconstruction area: $t = 5.157$; $P < 0.001$) and invested more adhesive silk in terms of mean spiral length per web ($t = 3.947$; $P = 0.001$) than did *Z. geniculata*, although the total web area

($t = 1.122$; $P = 0.278$), cumulative linear investment ($t = 2.295$; $df = 3,5$; $P = 0.094^*$), adhesive thread density ($t = -1.077$; $P = 0.298$) and the frequency of reconstructions ($Z = 1,076$; $P = 0.327$) is similar between species. Unfed *M. rogenhoferi* also reconstructed larger portions of their webs than did *Z. geniculata* (reconstruction area: $t = 7.700$; $P < 0.001$) although the total web area is again similar between species ($t = -0.457$; $P = 0.653$). *Metazygia rogenhoferi* invested more adhesive silk in terms of cumulative linear investment ($t = 4.880$; $df = 3,1$; $P = 0.016^*$) and mean spiral length per web ($t = 6.077$; $P < 0.001$) than did *Z. geniculata*. *Metazygia rogenhoferi* produced a slightly denser mesh of adhesive threads ($t = -2.165$; $P = 0.046$) than that of *Z. geniculata*, but the P -value could be less or even not significant if we had a greater sample.

DISCUSSION

Web site tenacity.—The cribellate *Z. geniculata* is more tenacious than the ecribellate *M. rogenhoferi*, the former seeming quite indifferent to changes in diet. On the one hand, *Zosis geniculata* began to abandon their webs only after a long period of starvation, a pattern also observed among other costly web weavers, such as the ecribellate, giant nephilid orbweavers (Vollrath 1985; Vollrath & Houston 1986) or some sheetweb weavers (Janetos 1982, 1986). On the other hand, the deinopoid clade also presented some web reductions associated with more mobile species (Lubin 1986). High tenacity seems thus to be associated with costly webs, independent of the type of adhesive thread, viscid or otherwise. These results give support to the hypothesis that the high diversity of Araneoidea is not simply the result of the discovery and use of viscid threads. The evolutionary reduction of site tenacity, made possible after the appearance of a less costly orb web (see below), could be a mechanism facilitating speciation, because it allowed a fast and opportunistic exploitation of new resources that is the ancestral condition promoting orb web spider high Triassic diversification (Vollrath & Selden 2007).

Silk investment.—In general, *M. rogenhoferi* is less responsive to a reduction in diet than *Z. geniculata*. While the uloborid species decreases silk investment, the araneid species does not alter its web investment, at least not in terms of the total length of silk (we did not test if thickness of threads or amount of glue changed). The results with *M. rogenhoferi* contradict previous studies with ecribellate orb weavers. Sherman (1994) showed that hungrier *Larinioides cornutus* (Clerck 1757) (Araneidae) invest more effort in foraging (web), and Higgins & Buskirk (1992) showed that *Nephila clavipes* (L. 1757) (Nephilidae) build larger orbs during times of decreased prey capture. Nevertheless, Crews & Opell (2006) found that *Cyclosa turbinata* (Walckenaer 1842) (Araneidae) does not change the investment in capture silk length, but progressively decreases its adhesive silk investment (less hygroscopic compounds) in successive webs built in harsh unfed conditions. Thus the literature does not present a simple pattern, probably as a result of the use of different feeding regimes in the different studies. It is not unreasonable for these orb weavers to present contradicting responses to different levels of starvation since it is not unusual to find nonlinear reaction norms (Schlichting & Pigliucci 1998). Therefore, these contradictory data can be the result of different researchers inspecting different regions of the same nonlinear reaction norm.

The goal of the present paper, however, was not to compare cribellate versus ecribellate complete reaction norms, but rather to test predictions in a more narrow phenotypic space. In this narrower context, we expected that the more costly webs of the uloborid would lead to a more conservative strategy, and the reduction in silk investment is in accord with this prediction. *Zosis geniculata* is able to reduce silk investment in response to reductions in prey number because of the properties of its adhesive thread. Cribellate silk keeps its adhesiveness longer than ecribellate silk (Eberhard 1980; Peters 1987; Sherman 1994, but see Opell & Schwend 2008), so that the web remains functional for longer periods, and the spider does not need to fully destroy the previous web in order to reconstruct the next one. At each reconstruction, the spider destroys only a part of the old web where it builds the new one; the final trap is a composition of many successive reconstructions. Eberhard (1971) observed a similar reconstruction pattern in *Uloborus diversus* Marx 1898 (Uloboridae), so it seems that these cribellate orb weavers handle reductions in prey supply using their longer lasting capture thread. They can reduce costs by staying at the same site and keeping the old trap for a longer period, a strategy that may not work well with the short lasting webs of the ecribellate orb weavers. In this way, silk investment is tied to web site tenacity. These cheap viscid orb weavers and wandering spiders may have had an advantage in relation to their cribellate counterparts during the spread of new prey resources during the Neopteran radiation (Vollrath & Selden 2007).

Other considerations.—Bond & Opell (1998) showed that the Araneoidea clade is statistically more diversified in species number than its sister group, the Deinopoidea, arguing that it was due to a key innovation: the invention of the viscid thread. According to Vollrath & Selden (2007) a flexible behavior lead to a faster exploration of new resources and the fine performance adaptations came after. So, we have suggested that our web site tenacity hypothesis is one possible flexible behavioral component that drives the orb web spider evolution followed by “morphological” (web) fine performance adaptation.

A recent phylogeny of Nephilidae (57 species, Kuntner et al. 2008) proposes that these spiders could be sister to the remaining Araneoidea (11199 species, Platnick 2008). Using the analysis proposed by Slowinski & Guyer (1993), we can see a clade imbalance, with the “remaining Araneoidea” being much more speciose than the family Nephilidae ($P = 0.005$). Thus, if this new positioning of Nephilidae proves to be correct, the greater species richness of Araneoidea would be associated with a clade within Araneoidea where the viscid thread is plesiomorphic.

Besides using a viscid thread, nephilids build unusually large webs. That a nephilid reconstructs only a sector of its web each time indicates that this web is costly and that it is economizing (Nentwig & Spiegel 1986). Also, most nephilids build other costly silken structures that are presumably not recycled (Kuntner 2006; Kuntner et al. 2008). Probably as a result of this costly web, these spiders also present high web site tenacity, even when subjected to a few prey (Vollrath 1985; Vollrath & Houston 1986).

Our comparison of two species, even ones carefully chosen to have similar life cycle, size, and web characteristics, certainly is not sufficient to establish broad trends. However,

our findings offer small but important experimental support for a novel hypothesis. Considering all the facts presented, we suggest that one of the factors driving the diversification of the Araneoidea clade might be the site tenacity reduction allowed by the less costly araneids' viscid webs, a complementary hypothesis to the widespread evolutionary explanations that present only the viscid silk performance as the main key innovation of orb weavers.

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