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Article Addendum

Fecundity increase supports adaptive radiation hypothesis in spider web evolution

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Identifying the mechanisms driving adaptive radiations is key to explaining the diversity of life. The extreme reliance of spiders upon silk for survival provides an exceptional system in which to link patterns of diversification to adaptive changes in silk use. Most of the world's 41,000 species of spiders belong to two apical lineages of spiders that exhibit quite different silk ecologies, distinct from their ancestors. Orb spiders spin highly stereotyped webs that are suspended in air and utilize a chemical glue to make them adhesive. RTA clade spiders mostly abandoned silk capture webs altogether. We recently proposed that these two clades present very different evolutionary routes of achieving the same key innovation—escape from the constraints imposed by spinning webs that contain a relatively costly type of physically adhesive cribellate silk. Here, we test the prediction that orb and RTA clade spiders are not only more diverse, but also have higher fecundity than other spiders. We show that RTA clade spiders average 23% higher fecundity and orb spiders average 123% higher fecundity than their ancestors. This supports a functional link between the adaptive escape from cribellate silk and increased resource allocation to reproduction in spiders.

Adaptative radiations explain much of the modern earth's diversity of life.[1,2] Yet, identifying the mechanisms driving the success of those radiations is difficult.[3-5] Spiders provide an exceptional system in which to test links between putative adaptations and patterns of speciation because of their extreme reliance on silk. Spider webs epitomize the adaptive use of high performance biomaterials in animal architecture.[6,7] All of the world's 41,000+ species of spiders spin silk fibers with strength to weight ratios up to five times greater than steel. Thus, it is not surprising that the spectacular evolutionary and ecological success of spiders is generally attributed to key innovations in the production and use of different silks.[8-12] The aerial orb webs of the Orbiculariae are one such example, which utilize a composite architecture including a framework of stiff, exceedingly strong major ampullate silk radii to suspend a highly elastic capture spiral coated with droplets of liquid glue (Fig. 1). The capacity of orb webs to reliably absorb the high energy impact of flying prey helped to make orbicularian spiders dominant predators of aerial insects in many ecosystems.

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However, such silk production is not without cost. Silk threads are composed primarily of proteins and a single orb web can be as much as 0.1–1% of a spider's wet body mass.[13] Thus, replacing lost webs from body reserves is presumably expensive. Furthermore, some silks cost more energy to spin than others. In particular, the cribellate silk used as adhesive fibers in relatively primitive spider webs functions through van der Waals interactions and physical entanglement.[14,15] This contrasts with the chemically adhesive glycoproteins found in the aggregate glue droplets of modern orb spiders.[16] In a time and energy-consuming process, cribellate spiders physically comb out puffs of silk containing the hundreds to thousands of nanoscale fibrils required for adhesive function (Fig. 1A). Consequently, spiders that utilize cribellate silk tend to show high fidelity to individual webs. In contrast, most derived spiders have either abandoned capture webs entirely or evolved chemically adhesive, aggregate glue, which allows webs to be constructed quickly and for silk to be recycled when webs are taken down and consumed.[17,18] We recently used a total evidence based phylogeny of spiders to demonstrate that these two behavioral patterns of silk use are derived strategies that mark the two most successful clades of spiders—wandering hunter/ambushers in the RTA clade (~22,000 species) and the orb-weaving Araneoidea (~12,000 species). We suggested that "escape" from the constraints imposed by use of expensive cribellate silk was causally related to the latter adaptive radiations of RTA clade and Araneoidea, such that the evolutionary shifts away from the use of capture silk altogether, and to chemically adhesive glue, played an important role in shaping the diversification of modern spiders. In turn, the hypothesis predicts that adaptive changes in silk use should be accompanied by increased fecundity. Here, we test this prediction by examining the correlation between changes in web use and fecundity across spiders.

Comparing Spider Fecundity

Reproductive output of spiders, measured as clutch size, generally increases with body size of spiders, both within and among species.[19-21] Here, we present data on reproductive output from 343 species across 60 of the 105 extant families of spiders, representing all higher lineages (see appendix). Comparative data is best analyzed in a phylogenetic framework, such as independent contrasts, to control for the inflation of degrees of freedom that can occur when comparing close relatives.[22] However, this is not feasible for the current data because most spider phylogeny is largely unknown. Prior studies also show that the relationship between spider body size and fecundity is relatively similar regardless of the use of "raw" or phylogenetically independent data.[19,20] Therefore, we concentrate on the phenotypic data themselves, with an understanding that Type I error may be somewhat inflated by this approach.

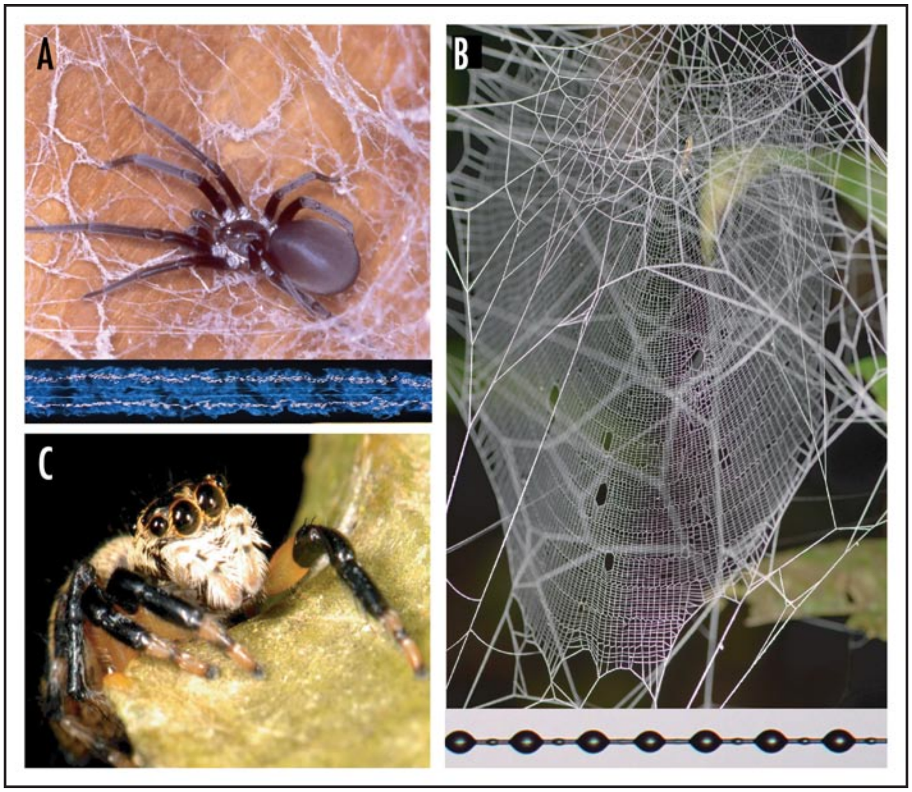

Figure 1. Spiders use silk in three broadly different strategies for prey capture. (A) Many spiders spin a variety of sheet webs with relatively amorphous architectures. These webs lack stereotyped major ampullate supporting threads and utilize cribellate adhesive threads (shown here in darkfield at the bottom of the panel). Cribellate silk consists of one or more pairs of core fibers surrounded by a sheath of nanoscale fibrils physically combed into puffs by the spider. (B) Nearly all orb weaving spiders and their relatives use stereotyped web spinning behaviors and defined frameworks of dragline silk to suspend webs relatively far from substrate. Thus, the form of the web is taxonomically rather than substrate specific. Most also utilize aggregate capture silk (see text). (C) RTA clade spiders tend to stalk or ambush prey, having abandoned the use of capture silks altogether.

Spider length was highly correlated with spider fecundity in a regression analysis ($R^2 = 0.49$, $p < 0.00001$)(Figure 2). We therefore used the standardized residuals of fecundity vs. body length to compare the reproductive output of orbicularian and RTA clade spiders versus all other taxa ("outgroup"). The lineage of spiders had a highly significant effect on residual fecundity (ANOVA $F_{2,340} = 40.4$, $p < 0.00001$). Both RTA clade and orbicularian spiders had higher fecundity than all other spiders (23 and 123% respectively). Furthermore, orbicularians were significantly more fecund than the RTA clade (Fig. 3).

While other factors also contribute to reproductive output, we argue that clutch size is a good overall estimator. Energy content of eggs is similar across a broad survey of spider taxa.[23] Many spiders can produce more than one clutch of eggs over their lifetime, but past studies suggest that individual clutch size strongly correlates positively with number of clutches.[21] Finally, there is currently no consensus on the potential for an egg size-number tradeoff within clutches, with near simultaneous studies proposing evidence for[20] and against the hypothesis.[19] Thus, single clutch remains at least a reasonably accurate estimator of overall spider reproductive effort.

Fecundity and Spider Evolution

The derived predatory behaviors considered here, development of aerial webs and loss of capture webs all together, are quite different. But, both allow "escape" from dependence on expensive cribellate silk.[12] Moreover, we show here that this escape is significantly correlated with increased reproductive output in both clades.

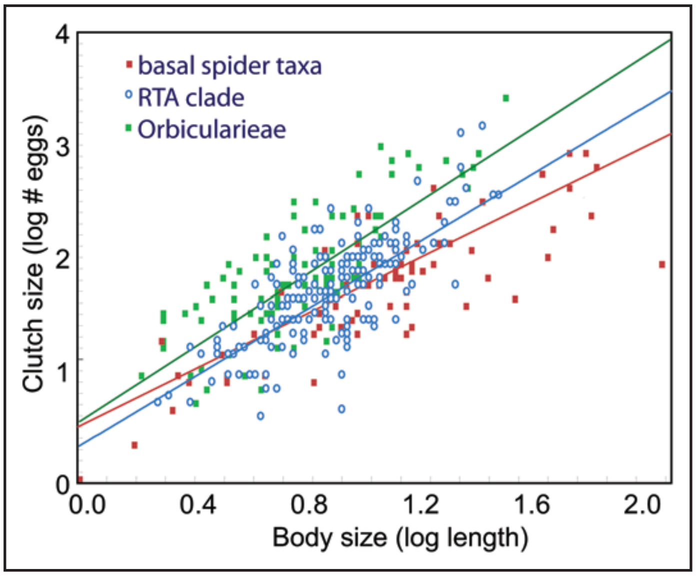

Figure 2. Log-log plot of clutch size versus body size in spiders.

AUTHOR: please refer to Figure 2 within the body text.

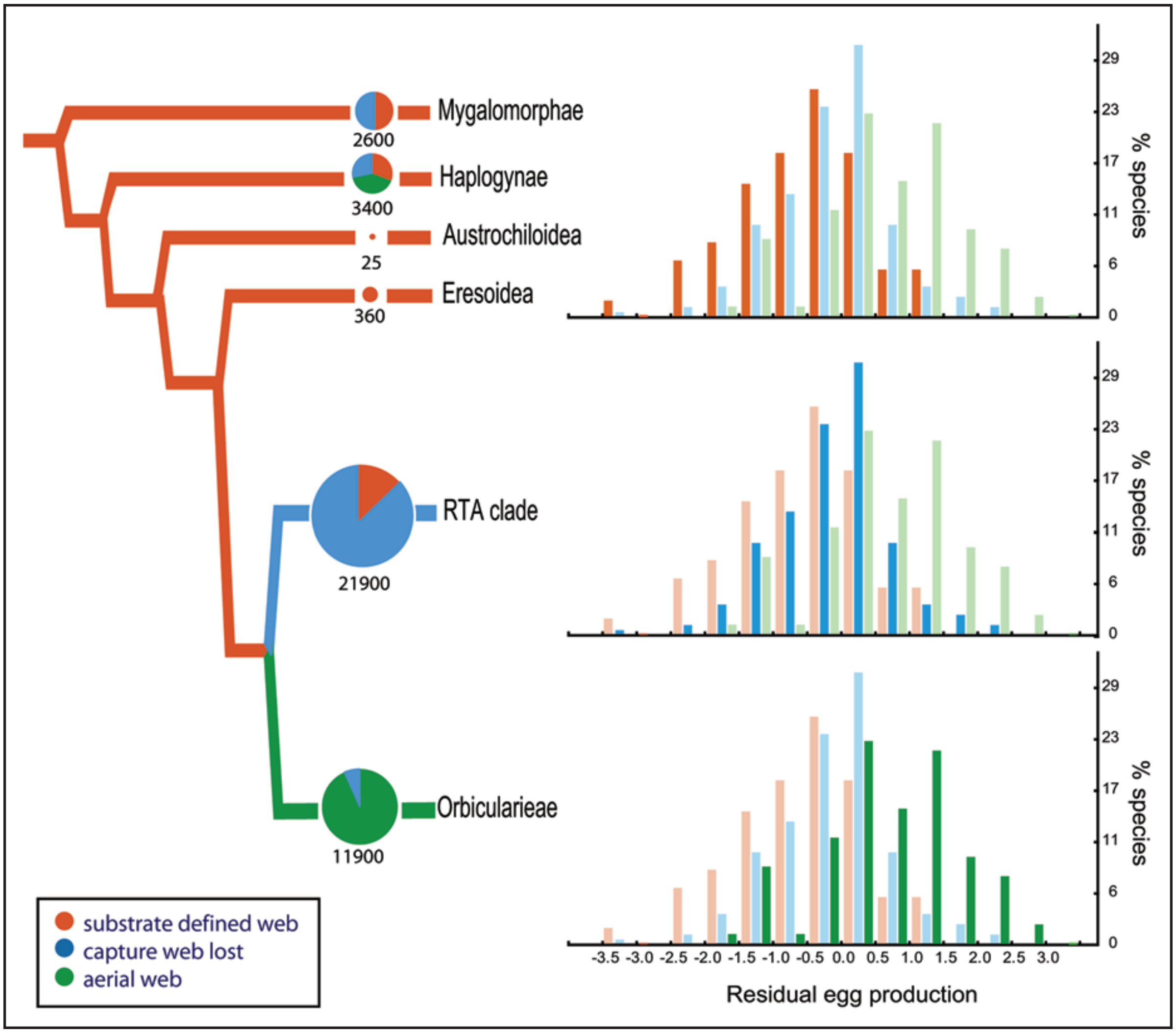

Figure 3. Relationship between fecundity and silk use by spiders. Residuals for egg production were calculated from the regression of individual clutch size on spider body length in Figure 2. The graphs show histograms of residual egg production for species within each of two highly successful, apical clades of spiders compared to all other taxa of spiders. The phylogeny is summarized from Blackledge et al. 2009 and illustrates the relationship between species diversity (total size of pie charts) and silk use ecologies (colors) among spiders.

The clutch sizes of orb spiders are much higher than either distant outgroup taxa or their sister lineage, the RTA clade (Fig. 3). The evolution of the stereotyped behaviors and the aerial frameworks of dragline silk used in the construction of orb webs may therefore have enabled access to a new source of abundant prey, flying insects, which neither hunter/ambushers nor primitive cribellate spiders can easily catch. Indeed, growing ecological data support the hypothesis that evolution has placed a premium on a fast growth life history for orb spiders. Positive, fecundity-based selection on female body size in orb spiders[24] necessitates high rates of prey capture.[25] Much of this biomass consumed by orbweavers is subsequently converted into egg production.[26,27] While spiders are famous for their low metabolic rates,[28] orb spiders are exceptions. Many orb spiders have notably higher metabolisms[29-31] and they require high rates of prey capture for survival and reproduction.[32] In contrast, some wolf spiders (RTA clade) and filistatids (an "outgroup" taxon in this study) can survive 200 days without food.[33] Thus, while the evolution of glue-coated orb webs represents a major evolutionary innovation in spiders that facilitates increased reproductive output; it may also have imposed a new set of ecological constraints that further shaped the evolution of silk use in these spiders.

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Appendix—Sources of Fecundity Data

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