

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.

Adaptive 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 Orbicularia 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.

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.

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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.

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 for²⁰ 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.

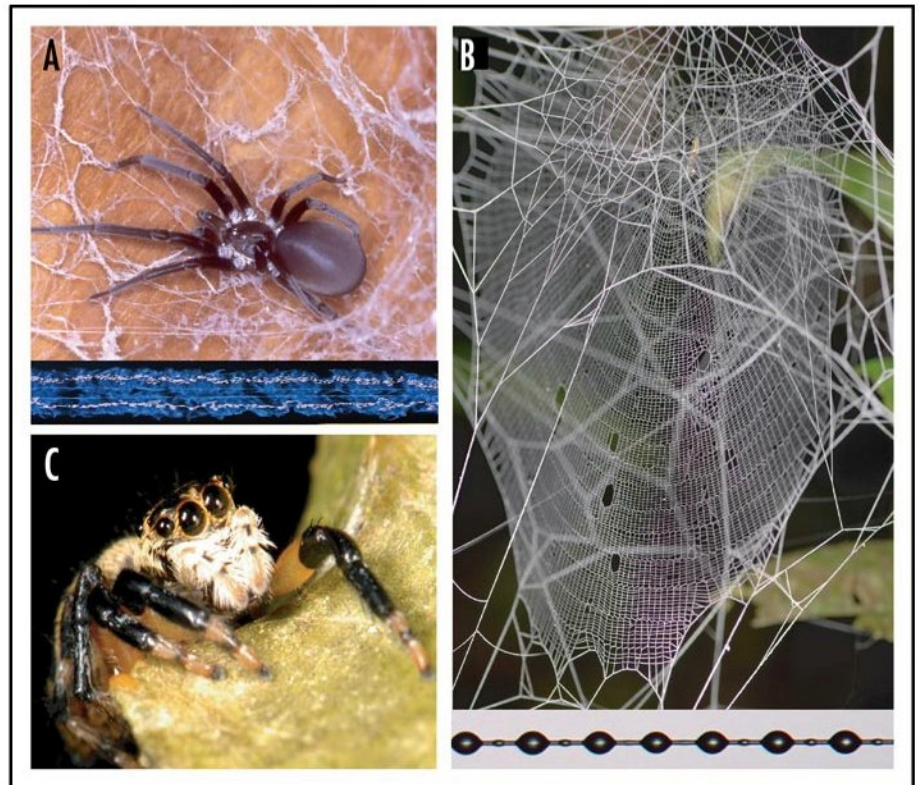


Figure 1. Spiders use silk in three broadly different strategies for prey capture. (A) Many spiders spin a variety of sheet webs with relatively amorphous architectures. These webs lack stereotyped major ampullate supporting threads and utilize cribellate adhesive threads (shown here in darkfield at 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.

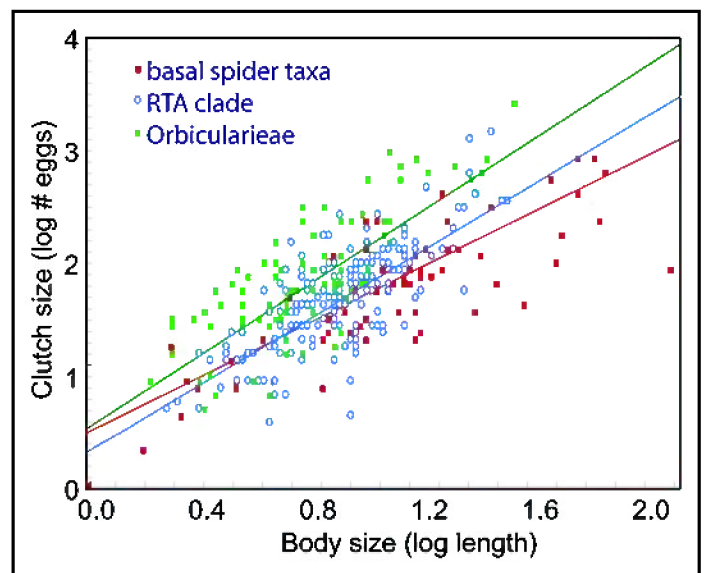


Figure 2. Log-log plot of clutch size versus body size in spiders.

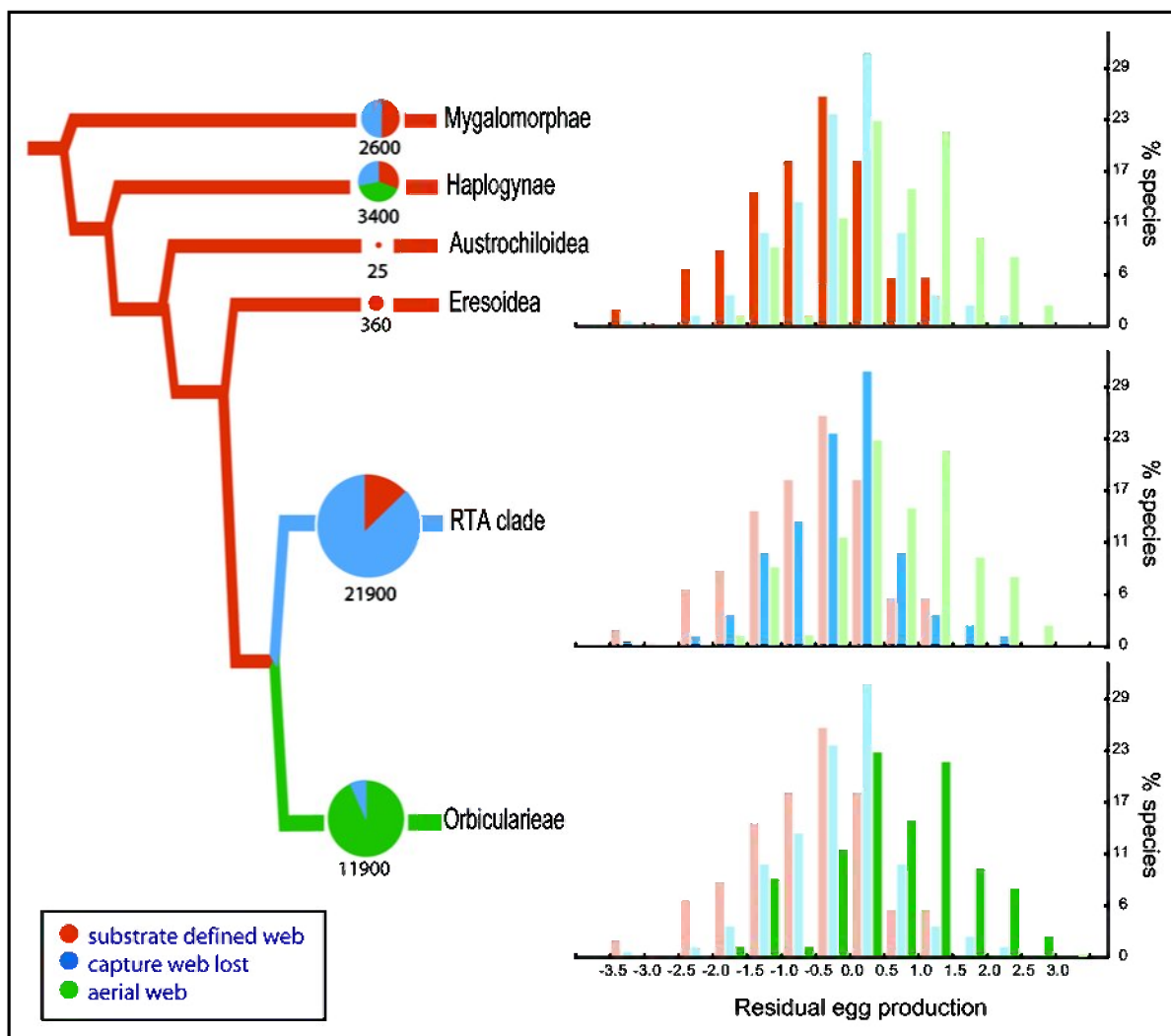


Figure 3. Relationship between fecundity and silk use by spiders. Residuals for egg production were calculated from the regression of individual clutch size on spider body length in Figure 2. The graphs show histograms of residual egg production for species within each of two highly successful, apical 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 spiders²⁴ 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 metabolisms²⁹⁻³¹ 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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References

1. Wagner WL, Funk VA, eds. Hawaiian biogeography: Evolution on a hot spot archipelago. Washington, DC: Smithsonian Institution Press 1995.
2. Orr MR, Smith TB. Ecology and speciation. *Trends Ecol Evol* 1998; 13:502-6.
3. Coddington JA. Cladistic tests of adaptational hypotheses. *Cladistics-Int J Willi Hennig Soc* 1988; 4:3-22.
4. Schluter D. *The ecology of adaptive radiation*. New York: Oxford University Press 2000.
5. Losos JB, Jackman TR, Larson A, de Queiroz K, Rodriguez-Schettino L. Contingency and determinism in replicated adaptive radiations of island lizards. *Science* 1998; 279:2115-8.

6. Denny M. Physical properties of spider's silks and their role in design of orb-webs. *J Exp Biol* 1976; 65:483-506.
7. Vollrath F. Spider Webs and Silks. *SciAm* 1992; 266:70-6.
8. Bond JE, Opell BD. Testing adaptive radiation and key innovation hypotheses in spiders. *Evolution* 1998; 52:403-14.
9. Blackledge TA, Coddington JA, Gillespie RG. Are three-dimensional spider webs defensive adaptations? *Ecology Letters* 2003; 6:13-8.
10. Craig CL. The significance of spider size to the diversification of spider-web architectures and spider reproductive modes. *Am Nat* 1987; 129:47-68.
11. Coddington J. The monophyletic origin of the orb web. In: Shear WA, ed. *Spiders: webs, behavior and evolution*. Stanford: Stanford University Press 1986; 319-63.
12. Blackledge TA, Scharff N, Coddington JA, Szüts T, Wenzel JW, Hayashi CY, Agnarsson I. Reconstructing web evolution and spider diversification in the molecular era. *Proc Natl Acad Sci USA* 2009; 106:5229-34.
13. Blackledge TA. Stabilimentum variation and foraging success in *Argiope aurantia* and *Argiope trifasciata* (Araneae: Araneidae). *J Zool* 1998; 246:21-7.
14. Hawthorn AC, Opell BD. van der Waals and hygroscopic forces of adhesion generated by spider capture threads. *J Exp Biol* 2003; 206:3905-11.
15. Opell BD. The ability of spider cribellar prey capture thread to hold insects with different surface features. *Funct Ecol* 1994; 8:145-50.
16. Vollrath F, Tillinghast EK. Glycoprotein glue beneath a spider web's aqueous coat. *Naturwissenschaften* 1991; 78:557-9.
17. Townley MA, Tillinghast EK. Orb web recycling in *Araneus cavaticus* (Araneae, Araneidae) with an emphasis on the adhesive spiral component, gabanide. *J Arachnol* 1988; 16:303-19.
18. Opell BD. Economics of spider orb-webs: the benefits of producing adhesive capture thread and of recycling silk. *Funct Ecol* 1998; 12:613-24.
19. Marshall SD, Gittleman JL. Clutch size in spiders: Is more better? *Funct Ecol* 1994; 8:118-24.
20. Simpson MR. Covariation of spider egg and clutch size: the influence of foraging and parental care. *Ecology* 1995; 76:795-800.
21. Enders F. Clutch size related to hunting manner of spider species. *Ann Entomol Soc Am* 1976; 69:991-8.
22. Harvey PH, Pagel MD. *The Comparative Method in Evolutionary Biology*. New York: Oxford University Press 1991.
23. Anderson JF. Energy Content of Spider Eggs. *Oecologia* 1978; 37:41-57.
24. Coddington JA, Hormiga G, Scharff N. Giant female or dwarf male spiders? *Nature* 1997; 385:687-8.
25. Higgins L. Female gigantism in a New Guinea population of the spider *Nephila maculata*. *Oikos* 2002; 99:377-85.
26. Eberhard WG. Rates of egg-production by tropical spiders in the field. *Biotropica* 1979; 11:292-300.
27. Wise DH. Food limitation of the spider *Linyphia marginata*: experimental food studies. *Ecology* (Tempe) 1975; 56:637-46.
28. Anderson JF. Metabolic Rates of Spiders. *Comparative Biochemistry and Physiology* 1970; 33:51.
29. Anderson JF, Prestwich KN. Respiratory gas exchange in spiders. *Physiol Zool* 1982; 55:72-90.
30. Anderson JF. Comparative energetics of comb-footed spiders (Araneae, Theridiidae). *Comp Biochem Physiol A-Physiol* 1994; 109:181-9.
31. Greenstone MH, Bennett AF. Foraging strategy and metabolic rate in spiders. *Ecology* 1980; 61:1255-9.
32. Venner S, Casas J. Spider webs designed for rare but life-saving catches. *Proc Roy Soc B* 2005; 272:1587-92.
33. Anderson JF. Responses to starvation in the spiders *Lycosa lenta* Hentz and *Filistata hibernalis* (Hentz). *Ecology* 1974; 55:576-85.
34. Brescovit AD, Raizer J, Amaral MEC. Descriptions and notes on the genus *Paradosenus* in the neotropical region (Araneae, Tetrachealidae). *J Arachnol* 2000; 28:7-15.
35. Costa FG, Perez-Miles F. Behavior, life cycle and webs of *Mecicobothrium thorelli* (Araneae, Mygalomorphae, Mecicobothriidae). *J Arachnol* 1998; 26:317-29.
36. Costa FG, Perez-Miles F. Reproductive biology of Uruguayan theraphosids (Araneae, Mygalomorphae). *J Arachnol* 2002; 30:571-87.
37. Coyle FA. A revision of the American funnel-web mygalomorph spider genus *Euagrus* (Araneae, Dipluridae). *Bull Amer Mus Nat Hist* 1988; 187:203-92.
38. Coyle FA, Oshields TC, Perlmutter DG. Observations on the behavior of the kleptoparasitic spider, *Mysmenopsis furtiva* (Araneae, Mysmenidae). *J Arachnol* 1991; 19:62-6.
39. Eberhard WG. Rates of egg-production by tropical spiders in the field. *Biotropica* 1979; 11:292-300.
40. Danielson-Francois AM. Natural history of *Glenognatha emertoni* (Araneae, Tetragnathidae): Mating behavior and sperm release in a haplogyne. *J Arachnol* 2006; 34:387-98.
41. Deng LL, Dai JY, Cao H, Xu MQ. Effects of an organophosphorous insecticide on survival, fecundity and development of *Hylyphantes graminicola* (Sundevall) (Araneae: Linyphiidae). *Environmental Toxicology and Chemistry* 2006; 25:3073-7.
42. Doran NE, Richardson AMM, Swain R. The reproductive behaviour of the Tasmanian cave spider *Hickmania troglodytes* (Araneae: Austrochilidae). *J Zool* 2001; 253:405-18.
43. Downes MF. The life-history of *Badumna candida* (Araneae, Amaurobioidea). *Aust J Zool* 1993; 41:441-66.
44. Edwards RL, Edwards EH, Edwards AD. Observations of *Theotima minutissimus* (Araneae, Ochyroceratidae), a parthenogenetic spider. *J Arachnol* 2003; 31:274-7.
45. Forster RR, Platnick NL. A review of the archaetid spiders and their relatives, with notes on the limits of the superfamily Palpimanoidea (Arachnida, Araneae). *Bull Amer Mus Nat Hist* 1984; 178:1-106.
46. Griswold CE, Meikle-Griswold T. *Archaeodictyna ulova*, new species (Araneae: Dictynidae), a remarkable kleptoparasite of group-living eresid spiders (Stegodyphus spp., Araneae: Eresidae). *American Museum Novitates* 1987; 2897:1-11.
47. Gundermann JL, Horel A, Roland C. Costs and benefits of maternal care in a subsocial spider, *Coelotes terrestris*. *Ethology* 1997; 103:915-25.
48. Hormiga G. A revision and cladistic analysis of the spider family Pimoidae (Araneidae: Araneae). *Smithsonian Contributions to Zoology* 1994; 549:1-104.
49. Kaston BJ. Spiders of Connecticut. State Geological and Natural History Survey of Connecticut 1981.
50. Kim KW, Roland C, Horel A. Functional value of matiphagy in the spider *Amaurobius ferax*. *Ethology* 2000; 106:729-42.
51. Fischer ML, Vasconcelos-Neto J. Parameters affecting fecundity of *Loxosceles intermedia* Mello-Leitao 1934 (Araneae, Sicariidae). *J Arachnol* 2005; 33:670-80.
52. Grismado CJ. A taxonomic revision of the spider genus *Ariadna audouini*, 1826 in Argentina and Chile, with the description of five new species (Arachnida, Araneae, Segestriidae). *Zoosystema* 2008; 30:333-60.
53. Griswold CE. A revision and phylogenetic analysis of the spider subfamily Phyxelidinae (Araneae, Amaurobioidea). *Bull Amer Mus Nat Hist* 1990; 3-206.
54. Guarisco H. Description of the egg sac of *Mimetus notius* (Araneae, Mimetidae) and a case of egg predation by *Phalacrotophora epeirae* (Diptera, Phoridae). *J Arachnol* 2001; 29:267-9.
55. Huber BA. Notes on the neotropical spider genus *Modisimus* (Pholcidae, Araneae), with descriptions of thirteen new species from Costa Rica and neighboring countries. *J Arachnol* 1998; 26:19-60.
56. Jocque R. A generic revision of the spider family Zodariidae (Araneae). *Bull Amer Mus Nat Hist* 1991; 1-160.
57. Cazier MA, Mortenson MA. Analysis of the habitat, web design, cocoon and egg sacs of the tube weaving spider *Diguetia canities* (McCook), (Araneae, Diguettidae). *Bulletin of the Southern California Academy of Sciences* 1962; 61:65-88.
58. Coyle FA, Meigs TE. Two new species of kleptoparasitic *Mysmenopsis* (Araneae, Mysmenidae) from Jamaica. *J Arachnol* 1989; 17:59-70.
59. Calderón R, Garrido M, Pinto C. Etapas del crecimiento de *Acanthogonatus frankkii* Karsch, 1880 (Araneae: Nemesiidae). *Revista Chilena Entomología* 1990; 18:19-24.
60. Bennett RG. Systematics and natural history of *Wadotes* (Araneae, Agelenidae). *J Arachnol* 1987; 15:91-128.
61. Baerg WJ. Tarantula studies. *Journal of the New York Entomological Society* 1938; 46:31-43.
62. Bentzien MM. Biology of the spider *Diguetia imperiosa*. *The Pan-Pacific entomologist* 1973; 49:110-23.
63. Bristowe WS. *The comity of spiders*. London: The Ray Society 1939.
64. Forster RR, Forster LM. *Spiders of New Zealand*. Dunedin: University of Otago Press 1999.
65. Ihara Y. *Cybaeus jinsekiensis* n. sp., a spider species with protogynous maturation and mating plugs (Araneae: Cybaeidae). *Acta Arachnologica* 2006; 55:5-13.
66. Huff RR, Coyle FA. Systematics of *Hypochilus sheari* and *Hypochilus coylei*, two Southern Appalachian lampshade spiders (Araneae, Hypochilidae). *J Arachnol* 1992; 20:40-6.
67. Girault AA. Standards of the number of eggs laid by spiders—I (Arach.). *Entomol News* 1911; 22:461-2.

Appendix—Sources of Fecundity Data

1. Amalin DM, Reiskind J, Pena JE, McSorley R. Predatory behavior of three species of sac spiders attacking citrus leafminer. *J Arachnol* 2001; 29:72-81.
2. Aviles L, McCormack J, Cutter A, Bukowski T. Precise, highly female-biased sex ratios in a social spider. *Proc R Soc Lond Ser B-Biol Sci* 2000; 267:1445-9.
3. Bond JE, Opell BD. Systematics of the spider genera *Mallos* and *Mexilia* (Araneae: Dictynidae). *Zool J Linn Soc* 1997; 119:389-445.
4. Bukowski TC, Christenson TE. Natural history and copulatory behavior of the spiny orbweaving spider *Micrathena gracilis* (Araneae, Araneidae). *J Arachnol* 1997; 25:307-20.
5. Coddington JA. The genera of the spider family Theridiosomatidae. *Smithsonian Contributions to Zoology* 1986; 1-96.
6. Coyle FA, Icenogle WR. Natural-History of the Californian Trapdoor Spider Genus *Aliatypus* (Araneae, Antrodiaetidae). *J Arachnol* 1994; 22:225-55.
7. Bosselaers J, Jocque R. Studies in Corinnidae: transfer of four genera and description of the female of *Lessertina mutica* Lawrence 1942. *Tropical Zoology* 2000; 13:305-25.
8. Boulton AM, Polis GA. Phenology and life history of the desert spider, *Diguetia mojavea* (Araneae, Diguettidae). *J Arachnol* 1999; 27:513-21.

43. Girault AA. Standards of the number of eggs laid by spiders (Aran.)—III. Entomol News 1914; 25:66-7.
44. Gertsch WJ, Platnick NI. A revision of the spider family Mecicobothriidae (Araneae, Mygalomorphae). American Museum Novitates 1979; 2687:1-32.
45. Paz N. Aspectos de la biología reproductiva de *Linothele megatheloides* (Araneae: Dipluridae). J Arachnol 1993; 21:40-9.
46. de Andrade RMG, Lourenço WR, Tambourgi DV. Comparison of the fertility between *Loxosceles intermedia* and *Loxosceles laeta* spiders (Araneae, Sicariidae). J Arachnol 2000; 28:245-7.
47. Fergusson IC. Natural history of the spider *Hypochilus thorelli* Marx (Hypochilidae). Psyche (Cambridge) 1972; 79:179-99.
48. Levi HW. Orb-weaving spiders *Actinosoma*, *Spilasma*, *Micrepeira*, *Pronous* and four new genera (Araneae: Araneidae). Bulletin of the Museum of Comparative Zoology 1995; 154:153-211.
49. Labarque FM, Ramírez MJ. Description of the female of *Drymusia serrana* Goloboff & Ramírez, 1991 (Araneae: Drymusidae) with notes on its biology. Zootaxa 2007; 1580:27-33.
50. Levi HW. The neotropical orb-weaving spiders of the genera *Wixia*, *Pozonia* and *Ocrepeira* (Araneae: Araneidae). Bulletin of the Museum of Comparative Zoology 1993; 153:47-141.
51. Levi HW. The Neotropical and Mexican species of the orb-weaver genera *Araneus*, *Dubiepeira* new genus, and *Aculepeira* (Araneae: Araneidae). Bulletin of the Museum of Comparative Zoology 1991; 152:167-315.
52. Levi HW. The bolas spiders of the genus *Mastophora* (Araneae: Araneidae). Bulletin of the Museum of Comparative Zoology 2003; 157:309-82.
53. Levi HW. The American orb-weaver genera *Larinia*, *Cercidia* and *Mangora* north of Mexico (Araneae, Araneidae). Bulletin of the Museum of Comparative Zoology 1975; 147:101-35.
54. Levi HW. The orb-weaver genera *Araniella* and *Nuctenea* (Araneae: Araneidae). Bulletin of the Museum of Comparative Zoology 1974; 146:291-316.
55. Marshall SD, Gittleman JL. Clutch size in spiders: Is more better? Funct Ecol 1994; 8:118-24.
56. Marshall SD, Uetz GW. The growth and maturation of a giant spider: *Theraphosa leblondii* (Latreille, 1804) (Araneae, Theraphosidae). Revue Arachnologique 1993; 10:93-103.
57. Lubin YD, Eberhard WG, Montgomery GG. Webs of *Miagrammopes* (Araneae: Uloboridae) in the neotropics. Psyche (Cambridge) 1978; 85:1-23.
58. Maddison WP. *Pelegrina franganillo* and other jumping spiders formerly placed in the genus *Metaphidippus* (Araneae: Salticidae). Bulletin of the Museum of Comparative Zoology 1996; 154:215-368.
59. Main BY. Biology of aganippine trapdoor spiders (Mygalomorphae: Ctenizidae). Aust J Zool 1957; 5:402-73.
60. McLay CL, Hayward TL. Reproductive biology of the intertidal spider *Desis marina* (Araneae: Desidae) on a New Zealand rocky shore. Journal of Zoology (London) 1987; 211:357-72.
61. Miyashita T. Growth, egg production and population density of the spider, *Nephila clavata* in relation to food conditions in the field. Res Popul Ecol 1986; 28:135-50.
62. Miyashita K. Life cycle of *Oecobius annulipes* Lucas (Araneae: Oecobiidae) under indoor conditions and the effect of photoperiod on nymphal development. Acta Arachnologica 1992; 41:5-10.
63. Nielsen E. The Biology of Spiders. Vol. 1. Copenhagen, Denmark: Levin & Munksgaard 1931.
64. Opell BD, Beatty JA. The nearctic Hahnidae (Arachnida: Araneae). Bulletin of the Museum of Comparative Zoology 1976; 147:393-433.
65. Opell BD, Berger AM, Shaffer RS. The body size of the New Zealand orb-weaving spider *Waikeana waitakerensis* (Uloboridae) is directly related to temperature and affects fecundity. Invertebrate Biology 2007; 126:183-90.
66. Prenter J, Elwood RW, Montgomery WI. Sexual size dimorphism and reproductive investment by female spiders: A comparative analysis. Evolution 1999; 53:1987-94.
67. Salomon M, Lubin Y. Cooperative breeding increases reproductive success in the social spider *Stegodyphus dumicola* (Araneae, Eresidae). Behav Ecol Sociobiol 2007; 61:1743-50.
68. Edwards RL, Edwards AD. Life history and ecology of the armored spider *Monoblennum muchmorei* (Araneae, Tetrablemmidae). J Arachnol 2006; 34:599-609.
69. Reichling SB, West RC. A new genus and species of Theraphosid spider from Belize (Araneae, Theraphosidae). J Arachnol 1996; 24:254-61.
70. Schick RX. The crab spiders of California (Araneidae, Thomisidae). Bull Amer Mus Nat Hist 1965; 129:1-180.
71. Punzo F, Henderson L. Aspects of the natural history and behavioural ecology of the tarantula spider *Aphonopelma hentzi* (Girard, 1854) (Orthognatha, Theraphosidae). Bull Br Arachnol Soc 1999; 11:121-8.
72. Platnick NI, Schwendinger PJ, Steiner H. Three new species of the spider genus *Liphistius* (Araneae, Mesothele) from Malaysia. American Museum Novitates 1997; 3209:1-13.
73. Platnick NI. A revision of the spider genus *Segestrioides* (Araneae, Diguetaeidae). American Museum Novitates 1989; 2940:1-9.
74. Platnick NI. A revision of the South American spider genus *Trachelpachys* (Araneae, Clubionidae). American Museum Novitates 1975; 2589:1-25.
75. Ono H. Spiders of the genus *Heptathela* (Araneae, Liphistiidae) from Vietnam with notes on their natural history. J Arachnol 1999; 27:37-43.
76. Schneider JM, Salomon M, Lubin Y. Limited adaptive life-history plasticity in a semelparous spider, *Stegodyphus lineatus* (Eresidae). Evol Ecol Res 2003; 5:731-8.
77. Suter RB. Determinants of fecundity in *Frontinella pyramitela* (Araneae, Linyphiidae). J Arachnol 1990; 18:263-9.
78. Watanabe T. Life history and seasonal change in the frequency of dimorphic stabilimenta of the orb-web spider, *Octonoba sylvatica* (Uloboridae). Acta Arachnologica 2000; 49:1-12.
79. West HB, Toft S. Last-male sperm priority and the mating system of the haplogyne spider *Tetragnatha extensa* (Araneae: Tetragnathidae). J Insect Behav 1999; 12:433-50.
80. Loch A, Yanez M, Vazquez I. Distribution and natural history of Mexican species of *Brachypelma* and *Brachypelmides* (Theraphosidae, Theraphosinae) with morphological evidence for their synonymy. J Arachnol 1999; 27:196-200.
81. Schutz D, Taborsky M. Mate choice and sexual conflict in the size dimorphic water spider *Argyroneta aquatica* (Araneae, Argyronetidae). J Arachnol 2005; 33:767-75.
82. Schwendinger PJ. Two new species of the arboreal trapdoor spider genus *Sason* (Araneae: Barychelidae) from Southeast Asia. Raffles Bulletin of Zoology 2003; 51:197-207.
83. Smith DR. Notes on the reproductive biology and social behavior of two sympatric species of *Philoponella* (Araneae, Uloboridae). J Arachnol 1997; 25:11-9.
84. Stiles GJ, Coyle FA. Habitat distribution and life history of species in the spider genera *Theridion*, *Rugathodes* and *Wamba* in the Great Smoky Mountains National Park (Araneae, Theridiidae). J Arachnol 2001; 29:396-412.
85. Vetter RS, Cokendolpher JC. *Homalonychus theologus* (Araneae, Homalonychidae): Description of eggsacs and a possible defensive posture. J Arachnol 2000; 28:361-3.
86. Vincent LS. The natural history of the California turret spider *Atpoides riversi* (Araneae, Antrodiaetidae)—demographics, growth-rates, survivorship and longevity. J Arachnol 1993; 21:29-39.
87. Wang XP. A generic-level revision of the spider subfamily Coelotinae (Araneae, Amaurobiidae). Bull Amer Mus Nat Hist 2002; 3-150.
88. Shear WA. The spider family Oecobiidae in North America, Mexico and the West Indies. Bulletin of the Museum of Comparative Zoology 1970; 140:129-64.
89. Coyle FA. The Mygalomorph Spider Genus *Microhexura*. Bull Amer Mus Nat Hist 1981; 170:64-75.
90. Valerio CE. Spitting spiders (Araneae, Scytodidae, *Scytodes*) from Central America. Bull Amer Mus Nat Hist 1981; 170:80-9.
91. Lowrie C, Dondale CD. A Revision of the nigra Group of the Genus *Parosia* in North America (Araneae, Lycosidae). Bull Amer Mus Nat Hist 1981; 170:125-39.