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Sexual Size Dimorphism: Evolution and Perils of Extreme Phenotypes in Spiders

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Abstract

Sexual size dimorphism is one of the most striking animal traits, and among terrestrial animals, it is most extreme in certain spider lineages. The most extreme sexual size dimorphism (eSSD) is female biased. eSSD itself is probably an epiphenomenon of gendered evolutionary drivers whose strengths and directions are diverse. We demonstrate that eSSD spider clades are aberrant by sampling randomly across all spiders to establish overall averages for female (6.9 mm) and male (5.6 mm) size. At least 16 spider eSSD clades exist. We explore why the literature does not converge on an overall explanation for eSSD and propose an equilibrium model featuring clade- and context-specific drivers of gender size variation. eSSD affects other traits such as sexual cannibalism, genital damage, emasculation, and monogyny with terminal investment. Coevolution with these extreme sexual phenotypes is termed eSSD mating syndrome. Finally, as costs of female gigantism increase with size, eSSD may represent an evolutionary dead end.

INTRODUCTION

This review focuses on sexual size dimorphism (SSD) in spiders, particularly female-biased extreme SSD (eSSD, i.e., female to male body length $\geq$2.0). Spiders exhibit the greatest eSSD among terrestrial animals, and eSSD females may be 3–10 times larger than males (33, 43, 90, 117, 143); *Nephila constricta* females reach 11.44 times the size of males (86), and *Arachnura logio* females reach 14.8 (60). However, SSD itself is probably not selected as such (except in particular, rare situations), but is rather the gendered outcome of natural or sexual selection acting on each sex. Nevertheless, eSSD is a notable phenomenon, and in spiders, it is certainly correlated with unusual morphological or behavioral traits, such as sexual cannibalism, male self-sacrifice and spontaneous death, emasculation and remote copulation, genital mutilation and plugging, traumatic insemination, mate binding, male accumulation, mate guarding, opportunistic mating, and even oral sexual encounters. It seems likely that these phenotypes are consequences of eSSD. Therefore, the questions of where, how, and why this phenomenon occurs deserve review and study.

Selection for increased fecundity, and therefore large female size (54), although important, is probably not a sufficient explanation for eSSD. If size genes are autosomal, and male size is selectively neutral, then a phyletic increase in female size should drag male size along, thus never resulting in eSSD. Therefore, the explanation for eSSD must be more complex. Below, we argue that sex-specific drivers operating in synergy, and perhaps in conflict, under both natural and sexual selection probably all play a role (14, 38). This theoretical landscape is complex, and the rarity of eSSD and paucity of empirical data are additional obstacles. Nevertheless, female-biased size dimorphism is the rule within terrestrial arthropods, and extreme cases are intriguing evolutionary puzzles. We summarize current research on gendered size evolution in spiders and examine the coevolution of behaviors in relation to sexual size differences. We also propose novel, testable hypotheses, some of which are general and could apply to other eSSD organisms.

EXTREME SEXUAL SIZE DIMORPHISM IN OTHER ANIMALS

SSD in other animal groups, whether female or male biased, has been much studied and reviewed (16, 28, 29, 91, 95, 134, 146). Compared to eSSD spider clades, most animal species are roughly monomorphic, i.e., male and female sizes are the same or slightly different (38).

The 2.0 threshold for eSSD may be arbitrary, but it is objective, it is consistent with the literature to date, and it highlights interesting questions. Hundreds of thousands of species, especially terrestrial arthropods, demonstrate slightly to moderately female-biased SSD. SSD can be calculated from various measurements. Although body length is the most widely available, carapace length or width, first tibia + patella lengths, or other linear measurements all correlate (43, 86). Body mass is probably the best general statistic but is rarely available if broad comparisons are the goal (90). Also, because mass scales as the cube while other SSD measurements are linear, the comparable mass threshold should be approximately 8.0. Lovich & Gibbons (97) proposed the sexual dimorphism index (SDI) = SSD − 1 for cases with both male and female biases (38). Because spiders are almost always female biased, SSD is more intuitive than SDI.

Spiders aside, eSSD is rare in the animal kingdom. eSSD can arise through body size evolution in either or both sexes (**Figure 1*a***). The males of the cichlid fish *Lamprologus callipterus* are roughly three times the size of females (130). In contrast, black dragonfish (Stomiidae: *Idiacanthus*) females may be eight times the size of males. eSSD in marine organisms tends to involve parasite-like males who live inside, or attached to, their females, as is the case for anglerfish, many barnacles, copepods, isopods, mole crabs, some burrowing or brooding bivalves, bonellid echiurans, puelche oysters, and a few polychaetes (*Osedax* spp.), or are stages of hermaphroditic species in *Cycliophora*,

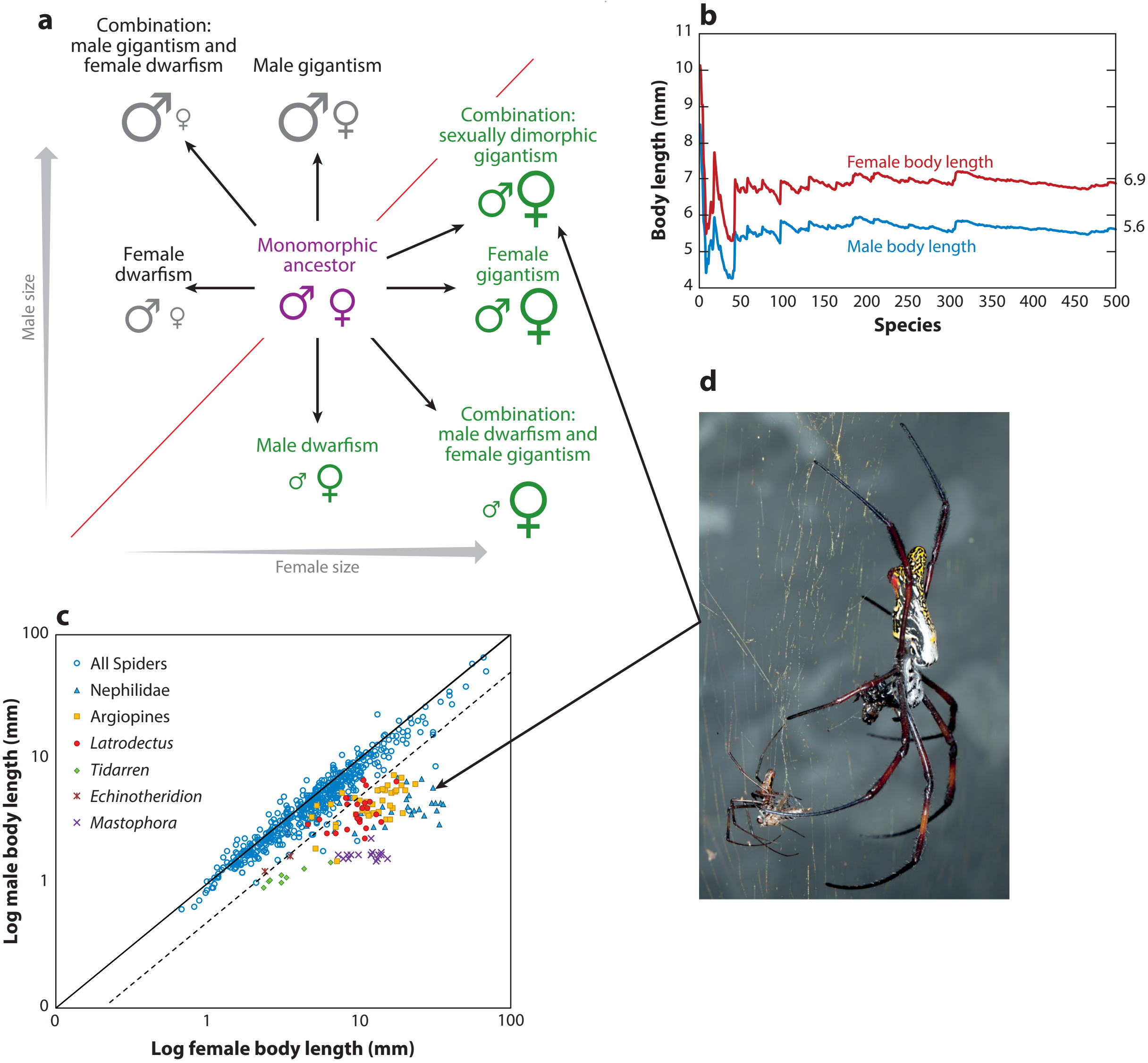


Figure 1

Spider size and the evolution of extreme sexual size dimorphism (eSSD). (*a*) Some potential pathways to SSD from monomorphism. The red line denotes isometry. The main possible scenarios are shown (more combinations are possible), but only those in green have been observed in spiders. (*b*) Running averages of male (5.6 mm) and female (6.9 mm) body length for a random sample of spider species ($n = 500$). (*c*) Male versus female spider size ($n = 500$). Fewer species are male biased (above the solid line of isometry); most are female biased. Argiopines, *Latrodectus*, *Tidarren*, and *Echinotheridion* are extremely female biased (below the dashed line of SSD = 2.0); nephilids and *Mastophora* are even more so. (*d*) The eSSD nephilid *Trichonephila inaurata*, linked with its likely explanation in panel *a* and with the size data in panel *c*.

sea cucumbers (*Leptosynapta clarki*), rotifers (Brachionidae), and the like (38, 99, 114, 142). eSSD marine species with free-living males are much rarer; an example is argonautoid octopods (135).

Among eSSD terrestrial animals, protected female lifestyles (i.e., sedentary in enclosed habitats) seem to be a trend. For example, queen ants and termites certainly lead protected lifestyles and can be huge. Some lampyrid and phengodid beetle females are wingless; have eSSD; and live in leaf litter, which perhaps offers more protection than other habitats. Bagworm female moths (Psychidae, particularly Oiketicinae) occasionally have eSSD; are wingless; and live in silken bags, arguably a protected habitat. Sternorrynchan bugs—scale insects, aphids, and relatives—often have sedentary large females and smaller motile males (31, 37). Among spiders, lineages with eSSD are overwhelmingly web spinners (26). Females are sedentary—prey, males, and relatively little else come to them. The web isolates them from terrestrial predators, and aerial predators find webs hard to bypass. However, orchid mantises (*Hymenopus coronatus*) have eSSD but do not live protected lifestyles [males are too small to be cannibalized (9)].

SEXUAL SIZE DIMORPHISM AND SPIDER BIOLOGY

Supplemental Material >

eSSD spider clades are exceptional among spiders. Based on a random sample of 500 species from the roughly 47,500 described (**http://wsc.nmbe.ch**), the running average of spider size stabilizes at 6.88 ± 8.5 (SD) mm for females and 5.61 ± 6.7 mm for males (**Figure 1*b***; **Supplemental Appendix 1**). The lower tail of this distribution, small spiders of either sex, is compact, but the opposite tail of big spiders is long; most size distribution outliers are large. Log-log plots of male and female body size predict that 86% of species are female biased, and 14% are male biased (**Figure 1*c***). Noteworthy eSSD clades are nephilids (Nephilidae; **Figure 1*d***), argiopines, mastophorines, *Caerostris* (Araneidae), *Latrodectus*, *Tidarren*, and *Echinotheridion* (Theridiidae).

Spider gender roles are predictable, but their sexual biology is unique (32). Sperm production occurs in the testes, but all males first ejaculate on sperm webs and suck up the sperm into their paired, uniquely modified hypodermic-like pedipalps, which are inserted into the female gonopore during insemination. All eSSD spider females are entelegyne: Their paired copulatory tracts lead to spermathecae for sperm storage that empty into a separate median canal where fertilization is believed to occur and through which eggs are laid. Spider sex is much more diverse than this textbook entelegyny (152), but it seems that no nonentelegynes have evolved eSSD.

Like any arthropod, spiders grow by molting. eSSD females grow larger than males by having shorter intermolt intervals and more molts before sexual maturity. Growth rate, time to maturity, and final body size pose trade-offs (15). Adult sizes ultimately vary due to total juvenile food consumption, but developmental plasticity and constraints are influential (58). Better-fed spiders molt quicker, but growth per molt is constrained (56). Conversely, poorly fed spiders prolong instars and therefore stay small and may not mature at all. Molt number variation in juvenile *Trichonephila clavipes* (58) and adult *Nephila pilipes* (90) suggest developmental plasticity. In both *Argiope* and *Trichonephila*, demographic conditions affect male maturation plasticity, and thus adult size; males are bigger in dense male populations but smaller around abundant females (69). These factors and the length of the growing season cause variation in adult size (57) as well as operational sex ratio (67). eSSD clades usually have male-biased operational and effective sex ratios (40, 125), which in turn increases sexual selection (69). However, the eSSD crab spider *Misumena* sex ratio is strongly female biased (59).

Female *N. pilipes* can molt facultatively after sexual maturity—a very rare ability in spiders (90). They grow by shedding most of their exoskeleton, but not the external or internal genitalia. Previously inseminated sperm can be retained, while body mass and presumably fecundity increase. Postmaturity molting females mated less often, whereas females that mated longer and with several males did not molt postmaturity (90). How females achieve this physiologically is unknown. Indeed, *N. pilipes* outliers occasionally set size records, even though their population mean is average due to range in female ages and instars. The tropical African *N. constricta*, sister to *N. pilipes*, may also molt after maturity. They show extreme variation in female, but not male, size (57).

Higgins and colleagues (57) tested multiple hypotheses to explain nephilid size variation. The usual developmental predictions failed. Species with larger sexes did not vary more in size, and male size variation did not correlate positively with female size (57). No comparable study exists for any other spider clade.

Differences in maturation time can result in siblings being disjunct in time. In aseasonal, tropical climates, disjunction would promote outbreeding, but disjunction is deleterious in seasonal climates (57). Being a large female in a seasonal climate means molting more and maturing later, risking male scarcity. Likewise, early males that scramble to adulthood to monopolize virgin females (30, 42) may die before the main breeding season.

PHYLOGENETIC OVERVIEW

Prior to the 1990s, spider SSD research used verbal arguments or evolutionary models that did not account for phylogeny. While some literature emphasizes small male size (30, 33, 43, 107, 110, 143), multiple pathways involving change in either sex could lead to an eSSD ratio. Male dwarfism, female gigantism, and combinations of these are all feasible (**Figure 1*a***).

Mapping gender size on an araneoid phylogeny inferred four (60) to nine (77) origins of eSSD. The families Araneidae, Phonognathidae, and Nephilidae seem to share a deep phylogenetic origin of eSSD (86). Within this large clade, groups have lost and regained eSSD repeatedly. Other clades evolved eSSD independently (e.g., the tetragnathid *Opadometa* and theridiids *Echinotheridion*, *Tidarren*, and *Latrodectus*). Newer, larger, and more robust phylogenies, as well as analytical tools and more empirical data, continue to appear, and, as usual, newer topologies alter the evolutionary picture.

Species phylogenies and good size data in nephilids and argiopines have provided more precise analyses of size evolution than analyses at the genus level or above. Only nephilids have a fairly complete species phylogeny (78, 86); argiopine phylogenies omit approximately half of the known species (23). In both, body size evolves rapidly and unpredictably at the species level (79). Again, the emerging macroevolutionary picture of gender size changes becomes increasingly complicated with newer topologies (86).

The pantropical golden orbweavers (*Nephila* and its relatives) are renowned for eSSD. Nephilidae is roughly 100 million years old (86) and contains 73 described species, although only 40 in total are expected after *Nephila* and *Trichonephila* are revised. Nephilid size evolution ranges from moderately SSD (1.4) to eSSD (11.4) (86). The nephilid ancestor was already eSSD, but both male and female size frequently change phyletically. Nephilid gigantism is linked to the evolution of web sizes and types, and therefore to lifestyles: Aerial and partially aerial webs facilitate, and tree-trunk webs constrain, eSSD (86). However, even this well-researched pattern poses more questions than it can solve. For example, it is the males (86), not the females (83), whose sizes significantly increase phyletically, and no relevant classical biological rules seem to apply to nephilid size.

The araneid silver-faced spiders (*Argiope*, *Gea*, *Neogea*) are second to nephilids in SSD research. 110 species of these largely tropical, colorful, diurnal, moderately SSD to eSSD spiders with ostentatious, silk-decorated webs are described (23–25). SSD apparently originated before *Argiopinae*, but size evolution stagnated over roughly 40 million years, and SSD steadily declined (23, 79). Araneidae certainly contains other intriguing eSSD lineages (124). However, few have been revised or analyzed phylogenetically. The eSSD *Caerostris* is a partial exception, although many undescribed species await description (49, 50, 75). Magalhães & Santos (100) provided a preliminary species phylogeny of *Micrathena* and inferred six independent origins of eSSD.

The phonognathids *Deliochus* and perhaps *Artifex* contain some eSSD species (66, 86). The tetragnathid *Opadometa fastigata* is eSSD. The other araneoid clades with eSSD species are all theridiids, *Latrodectus*, *Tidarren*, and *Echinotheridion* (77). However, phylogenies and good size data are lacking.

A few nonaraneoid, perhaps single, instances of eSSD species are known. The crab spiders *Mecaphesa celer*, *Misumena vatia*, *Misumenoides formosipes*, *Misumessus oblongus*, and *Thomisus onustus* (21, 54, 93) and the fishing spider *Dolomedes tenebrosus* (131) are examples of apparently single eSSD species in large clades. No doubt other eSSD spider species exist. Our random sample of 500 species discovered 9 new cases (**Supplemental Appendix 1**).

Supplemental Material >

SIZE EVOLUTION DRIVERS

Differential Equilibrium Model of Sexual Size Dimorphism

Tempo and patterns of eSSD can be clade or species specific, thwarting generalization. In a differential equilibrium model, SSD is the sum of several, possibly opposing, selective forces acting on each sex (14). **Figure 2** depicts a modification of this model allowing for tight (**Figure 2*a***), loose (**Figure 2*b***) and lost (**Figure 2*c***) genetic correlation between male and female sizes and lists the potential drivers of sex-specific size evolution that might affect male and female size and fitness in spiders. Below, we group these drivers into broad categories such as natural versus sexual selection (4), sexual conflict (113), and ecological factors. Depending on genetic correlation, the outcomes are monomorphism, moderate SSD, or eSSD (**Figure 2**).

Natural Selection

Fecundity selection (**Figure 2**) usually explains large female size in arthropods in general (14), and spiders in particular (43, 54, 118). In spiders, female body size and fecundity are tightly linked as in *Stegodyphus* (101) and in *Trichonephila* (58). However, experimental evidence for the overall fecundity advantage of large females in nephilids conflicts (83): Of the six scrutinized species, only three showed unequivocal fecundity advantages, yet none of these three were larger than the sizes reconstructed for their ancestors (83). The other three species showed no effect of size on fecundity and were smaller than their reconstructed ancestors. It seems that strong selection for fecundity maintains large female size, but weaker selection for fecundity correlates with phyletically smaller sizes. Comparable data in other clades are not yet available, and thus no generalization is possible.

Gendered foraging strategies and differential growth rates are two additional natural selection drivers of size evolution. Whether they are proximate causes for SSD (61) or consequences of SSD is unclear. Females have higher nutritional requirements than males, which should lead to different foraging (web) biologies and developmental trajectories. However, the first three to four instars and webs of both *Nephila* sexes are usually indistinguishable, suggesting that they target similar prey. Little support exists for intersexual niche divergence in spiders (144).

Gravity may shape size evolution (**Figure 2**). It probably sets an upper limit on female mass (size) above which web building and aerial foraging cannot function. Gravity may strongly select male size due to the energetics of mate searching (53, 107). Adult female web spiders are sedentary, and males must search, walk, climb, and traverse to find them (43). Smaller, or perhaps optimally sized, males should result (107, 108). However, some results refute this hypothesis (18). The hypothesis has been refined to apply to male bridging behavior (essentially lateral movements), not climbing, to select for size (27). Again, these predictions lack empirical support. Testing whether smaller males of the African hermit spider (*Nephilingis cruentata*) would have advantages in vertical climbing and horizontal bridging, Quiñones-Lebrón et al. (120) found that larger, not smaller, males were faster climbers and detected no differences in bridging ability across male sizes.

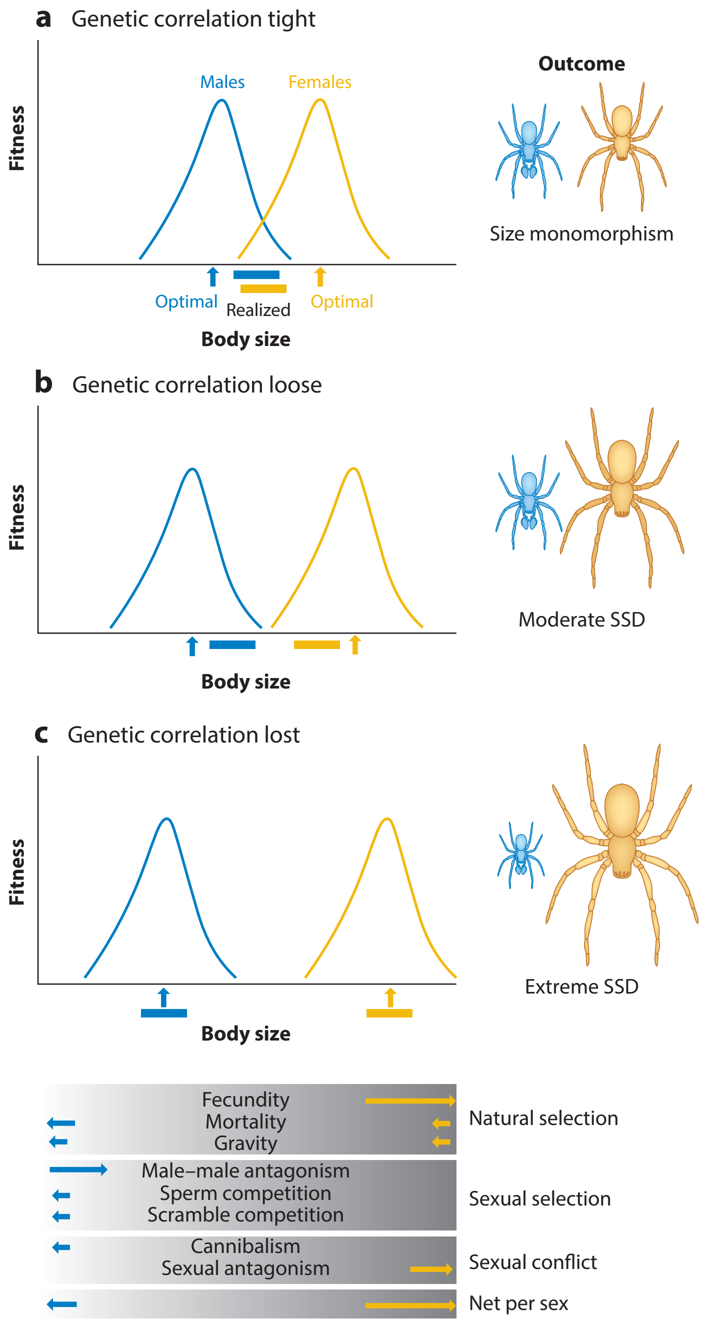


Figure 2

The differential equilibrium model of sexual size dimorphism (SSD) evolution. (*a*) If genetic correlation for size traits between males and females is tight, then the realized gender sizes are away from their optima, and the morphological outcome is size monomorphism. (*b*) If genetic correlation is loose, then the realized gender sizes are closer to, but do not reach, their optima, and the morphological outcome is moderate SSD. (*c*) If genetic correlation is lost, then the realized gender sizes align with their optima, resulting in extreme SSD. In the lower panel, the model allows for potential size evolution drivers in male and female spiders and their hypothetical directions and relative strengths.

The differential mortality hypothesis proposed that males, the mate-searching sex, died earlier and faster than females (143). This model assumed that the inability of investigators to relocate freely roving marked *T. clavipes* males was always due to mortality. If this is true, then selection might favor smaller male size (**Figure 2**). The model predicted male dwarfism in any species with sit-and-wait female and wandering male life histories and a female-biased operational sex ratio (143). However, field and experimental tests failed to support the hypothesis as a major explanation of eSSD (117, 119, 145), and comparative tests using phylogeny also refuted it (26, 60, 117). In *T. clavipes*, larger, not smaller, males reach females earlier (20). *Trichonephila* operational sex ratios are strongly male, not female, biased (45). Searching *Trichonephila fenestrata* males experienced only modest mortality risks (45), although data on *Trichonephila plumipes* suggest otherwise (68). Limited evidence thus supports the differential mortality hypothesis, even as a minor component of the differential equilibrium model (**Figure 2**).

Sexual Selection

Experimental studies in *Trichonephila* and *Phonognatha* confirm that larger males win competitions for access to females, but not in *N. pilipes* and *Nephilingis livida* (30, 72, 83). On the whole, direct male–male antagonism overwhelmingly selects for larger male size (**Figure 2**) and tends to decrease, not increase, eSSD (83).

Sperm and scramble competition represent other sexual selection mechanisms that may operate post- and precopulation (**Figure 2**). Scramble competition could favor protandrous males mating with more females sooner (55). Small size was no disadvantage to males of the giant wood spider (*N. pilipes*) in both scramble and sperm competition; these two drivers were interpreted to favor male dwarfism in this species (30). However, phylogenetic patterns complicate interpretation because *N. pilipes* males are larger than their ancestors (86). Indeed, protandry is typical of most males regardless of SSD (43) and therefore can only be a weak general explanation for SSD.

Evidence that sperm competition can drive small male size (**Figure 2**) is also preliminary. *Trichonephila edulis* and *Trichonephila inaurata* experience a small male advantage, while *N. pilipes* and *Trichonephila senegalensis* experience none (83). *T. senegalensis* males adjust their mating investment according to their competitive ability, the intensity of sperm competition, and female reproductive value (109), and this condition-dependent strategy maintains a considerable size variation in males. Thus, size-specific strategies enable the males of different sizes to achieve a similar average paternity.

Finally, female choice could select for smaller males. The hypothesis has only been tested in the context of sexual cannibalism (see below). In sum, the role of sexual selection on the evolution of eSSD remains ambiguous.

Sexual Conflict

If smaller males better evade their cannibalistic mates, or are simply not worth an attack nutritionally or energetically (150), then dwarf males would result (33). Sexual cannibalism is indeed common in eSSD spiders such as *Nephila*, *Trichonephila*, *Argiope*, and *Latrodectus*; cannibalism could generally explain small males (**Figure 2**). Nephilid experimental research is equivocal on increased survival of smaller males (83). Cannibalized *T. plumipes* males were indeed larger (128), but cannibalized *T. edulis* males were smaller (35, 65). To make things more complicated, sexual cannibalism may result from male self-sacrifice rather than overt female aggression. If it results from male self-sacrifice, then it is not sexually conflicted behavior (5). Even if due to female aggression, killing may occur pre- or postmating, the former being a radical form of female choice (36, 73). Not all female aggressive behaviors are obviously cannibalistic.

Fishing spiders (*Dolomedes*) are mostly monomorphic, but eSSD *D. tenebrosus* males spontaneously die in copula (131). The absence of female aggression calls into question the role of sexual conflict (133). Other, monomorphic *Dolomedes* females can be aggressive toward males prior to, during, or after copulation (8, 62, 64). In *Dolomedes triton* and *Dolomedes fimbriatus* intraspecific SSD variation and cannibalism were correlated, as larger, less dimorphic males survived female attacks more often (63, 70). Similarly, larger males of the relatively monomorphic *Araneus diadematus* better survived female aggression (123). These results question sexual cannibalism as the general cause of small male size, at least in low-SSD species. We return to the biology of sexual cannibalism below.

Sexual conflict over mating rates could cause runaway selection for eSSD, broadly termed sexually antagonistic coevolution (**Figure 2**). If fecundity selection produces moderate female-biased SSD initially via delayed female maturation, then potential outcomes could be (*a*) a male-biased sex ratio (45), (*b*) increased sexual selection (42), or (*c*) monogyny via paternity protection mechanisms (46). Paternity protection mechanisms involve genital plugging (137) and depressed female mating frequencies (80). Imposed monandry works against female interests; females resist by evolving adjustments in genital size and complexity (80, 98) to increase mating rates and by cannibalizing more males. Female body size can evolve to extremes (within constraints), which just reinforces these drivers. Such a sexual conflict ratchet could result in extreme gendered phenotypes, including female size. This hypothesis predicts positive correlations between eSSD and female mating rates and between eSSD and sexual cannibalism. While eSSD and cannibalism correlate broadly (see above), eSSD and mating rates are not significantly correlated in nephilids (80). Thus the sexually antagonistic coevolution receives partial support.

Ecological Factors

Nephilid phyletic sexual size and variation are poorly explained by broad-scale geographic factors (57). However, local ecological factors might explain some SSD in clades that show no clear phylogenetic trend, like *Argiope* (23, 24). However, landmass size, seasonality, altitude, and latitude effects on sexual size variation have not been comparatively investigated. The island rule predicts that island populations (of mammals) will become either larger or smaller than on the mainland (96). The converse Bergmann's rule predicts that cold-blooded animal body size will increase with temperature and thus decrease with latitude and altitude (17). Indeed, *Argiope argentata* females do get smaller with latitude, but males do not. Females are smaller on islands (island rule), and males are not (22). *A. argentata* females, but not males, respond as predicted to geography, probably as a proxy for temperature and seasonality. The actual targets of selection were not verified, but web site; prey availability; and predator, parasite, and kleptoparasite loads are all plausible.

EXTREME SEXUAL SIZE DIMORPHISM MATING SYNDROME

Web spiders with eSSD often have unusual mating biologies. In order of increasing sexual conflict, these traits include male accumulation, opportunistic mating, mate guarding, mate binding, genital mutilation, genital plugging, emasculation, and sexual cannibalism. The latter three at least coevolve with eSSD (77, 104, 149), and the eSSD mating syndrome (**Figure 3**) may encompass all of these phenotypes (77). Evolutionary arms races of gendered adaptations and counteradaptations can result (82, 94, 153), as predicted by sexually antagonistic coevolution (19, 140).

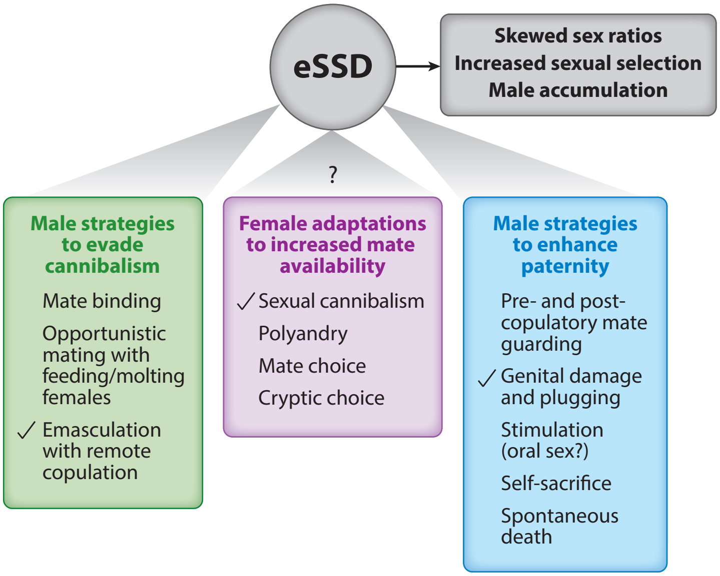


Figure 3

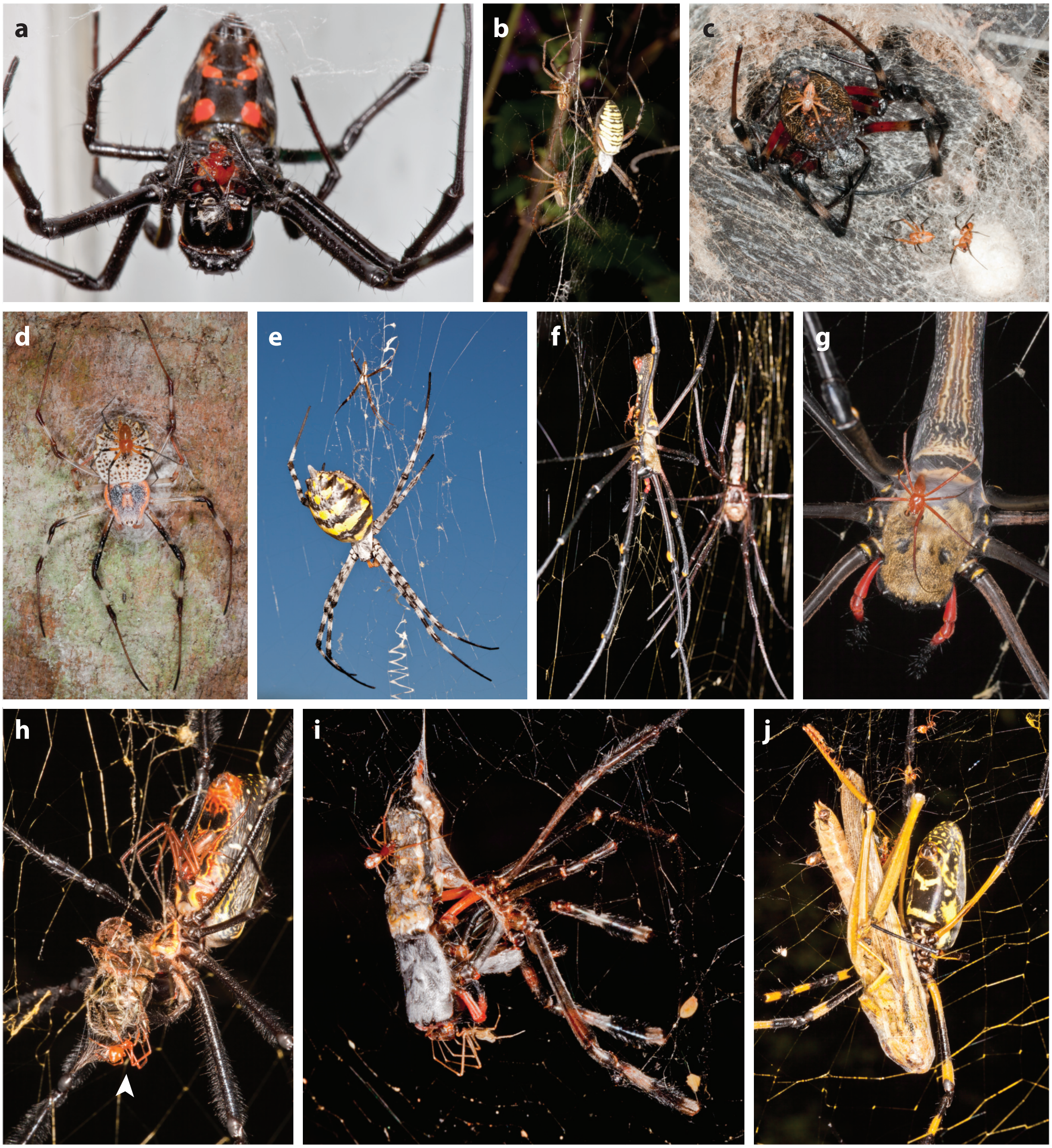
The extreme sexual size dimorphism (eSSD) mating syndrome. Male evasion of cannibalism and paternity protection strategies, and female behaviors to increase mate availability, may all co-occur with eSSD. Male-skewed operational sex ratios, male accumulation, and increased sexual selection are its consequences. Tick marks represent phenotypes that were shown to covary with eSSD.

Sexual Cannibalism

Cannibalism commonly occurs under certain ecological conditions in diverse animals (44), but sexual cannibalism (**Figure 4*a***) has a specific role. In eSSD animals, giant females may eat courting or mating males, often viewed as the ultimate conflict of interest (127). Sexual cannibalism implies that males suffer fitness costs. If male fitness somehow benefits, then it is instead male self-sacrifice (see below). The timing of sexual cannibalism is important. If precopulatory cannibalism measures mate quality (73), then postmating cannibalism is more likely a female adaptation to manipulate mating rates. Kuntner et al. (80) found a negative correlation between postcopulatory sexual cannibalism and male mating rates in nephilids. Sexual cannibalism probably enables a female to evade monopoly by a single male. Consistent behaviors support the inference that nephilid males do not benefit from being eaten after mating. They evade attacks (80), always place their bodies far from female jaws (unlike many other spiders), and flee if the female becomes aggressive (88). These behaviors may evade or depress female aggression and/or ameliorate decreases in male fitness (if not survival). Additional male behaviors work against cannibalism, like mate binding, remote copulation, mate guarding, and mating attempts when females are feeding or molting (82). Although not unique to eSSD lineages, sexual cannibalism strongly correlates with eSSD (77, 149). Experiments on moderately SSD species, like wolf and fishing spiders, show that cannibalism depends on individual SSD parameters: Big females attack smaller more often than larger males (70, 151). In sum, big females control their sexual encounters.

Male Self-Sacrifice

Male self-sacrifice is unusually common in eSSD spiders (104). In widows, cannibalized males copulate longer and fertilize more eggs (5). *Latrodectus hasselti* males intentionally twist their abdomens toward the female fangs and are eaten (6), but only during their second copulation. Widow spider males therefore benefit from being cannibalized. Cannibalized male fishing spiders (*D. tenebrosus*) also benefit. This eSSD species (unlike other *Dolomedes*) has male-biased sex ratios. Males are strictly monogynous, obligately and spontaneously die in copula, and suffer genital



(Caption appears on following page)

Figure 4 (*Figure appears on preceding page*)

Extreme sexual size dimorphism (eSSD) spider natural history. (*a*) Sexual cannibalism in *Nephilengys malabarensis*. (*b*,*c*) Male accummulation in (*b*) *Argiope bruennichi* and (*c*) *Nephilingis cruentata*. (*d*,*e*) Mate guarding in (*d*) *Herennia multipuncta* and (*e*) *Argiope australis*. (*f*) Opportunistic mating in *Nephila pilipes*, showing a male mating with a freshly molted female. (*g*) Mate binding of the female body in fine silk in *N. pilipes*. (*h*–*j*) Kleptoparasitism in (*h*) *Trichonephila fenestrata* and (*i*,*j*) *Trichonephila senegalensis*, resulting in the female host sharing a meal with a theridiid kleptoparasite (*h*, *arrow*) while feeding and mating, and the host female being killed and consumed by kleptoparasites during molting (*i*). (*j*) Giant females routinely feed on large invertebrate prey, but this often has to be shared with kleptoparasites. Image copyright M. Kuntner.

mutilation (131). That females eat their deceased partners suggests that males are self-sacrificing (132). Females that cannibalized males had more offspring of superior size and survivorship (133). However, while sacrificed males enjoy direct fitness benefits via paternal effort, their mating effort does not reduce sperm competition (133). That other *Dolomedes*, a global clade, are sexually monomorphic and not known for male self-sacrifice suggests that, in *D. tenebrosus*, self-sacrifice relates to eSSD.

Echinotheridion and *Tidarren* males, as well as males of a *Cyrtophora* species and at least one *Araneus* (*Araneus pallidus*), all self-sacrifice, as judged by lack of male behaviors to evade cannibalism (104).

Argiope males sacrifice themselves, and the offspring from cannibalism are more fit (147). However, *Argiope aurantia* males spontaneously die only after mating with both sperm transferring organs, thereby making female overt aggression prior to cannibalism moot (41). It seems that all studied *Argiope* males die spontaneously during copulation (126) and are eaten thereafter. As noted above, so do *D. tenebrosus* and *L. hasselti*. All cases may be terminal investments in paternity (7). However, sexual cannibalism and conflict can co-occur with male self-sacrifice and spontaneous death in the same species, and therefore, experimental research should specify the precise timing and context of the male's demise, i.e., during the male's first or second copulation. The former may imply fitness costs for the male, while the latter may not.

Male Accumulation, Mate Guarding, Opportunistic Mating

Male accumulation at female webs (**Figure 4*b*,*c***) results from sex-specific growth trajectories that lead to operational sex ratios being skewed toward males. Male accumulation is phylogenetically correlated with the evolution of eSSD in araneoids (104). Small males cohabit with juvenile females (**Figure 4*b***), sharing meals and awaiting her maturation. This strategy, termed precopulatory mate guarding, is also typical of eSSD clades. The highly male-biased sex ratio means that several to many males share each female web (**Figure 4*c***), thus potentially increasing sexual selection. Males compete fiercely and fight for the alpha position near the female (**Figure 4*c*–*e***). Typically, the closest male mates first; keeping rivals away is critical. When a female molts to sexual maturity, the alpha male usually mates with her while she is teneral (**Figure 4*f***), so-called opportunistic mating (42). Males are relatively safe; soft, molting females cannot attack (139). Mating with females while they are eating (**Figure 4*h***) is also opportunistic mating (47); by doing so, males run less risk of sexual cannibalism and injury.

Mate Binding

Male *N. pilipes* stereotypically lay silk threads on the female body and legs in between mating bouts (**Figure 4*g***), called mate binding (88). Mate binding lowers female aggression. Both tactile and chemical communication calms females, but tactile communication prevents attack more effectively (153). Males only use mate binding after copulation has been interrupted by female aggression. Mate-binding males usually relax the female enough to resume mating (153). Location matters in mate binding. A female can more easily attack the male if he is positioned ventrally, near her genitalia and jaws. Males only bind females dorsally, between their carapace and abdomen (**Figure 4*g***), never ventrally. Signaling to the female on her dorsal surface is safer and is probably an adaptation to avoid female aggression and cannibalism, thus increasing male mating frequency (153). Darwin's bark spider males (*Caerostris darwini)* also bind their mates, as do certain non-SSD species (51).

Genital Mutilation and Plugging

Female spiders benefit from polyandry by increasing the genetic variability of offspring and avoiding inbreeding (11). This may be especially true for giant, sedentary orbweaver females that attract males with pheromones. Multiple males compete for access to the female. Postcopulatory mate guarding (**Figure 4*c–e***) is one way to monopolize a female, but plugging of the female genital tract, by male genital breakage or even full emasculation, is another (82). Coin and hermit spider males—all approximately four times smaller than their females—use their severed genitalia physically to block females from remating (71, 72, 88, 89). Curiously, *N. pilipes* males have hair-like genitalic termini that are ineffective plugs, even though they break off inside the female (88). In nephilids with morphologically more complex palps, males effectively monopolize females (82), and in this group, genital complexity and female mating rates vary inversely (80).

Emasculation, Remote Copulation, and Traumatic Insemination

Small males may produce only enough sperm to fertilize the eggs of one large female. Genital plugs could prevent females from mating with rival males. Males will sacrifice one or both palps during or after mating, thereby becoming emasculated—effectively eunuchs (74, 76, 77). These eunuch males are superior fighters and fiercely defend the female from intruders (89). Eunuch male hermit spiders endure longer and fight more aggressively than intact males (71, 92). The severed palp stuck in the female genitalia still contains the male sperm reservoir, as well as the sclerites that help to transfer sperm. Severed palps continue to transfer sperm to the female, a process called remote copulation (94). Exactly how this occurs is unknown, but remote copulation is an additional way in which males increase reproductive success and counter sperm competition and sexual cannibalism. Other males traumatically inseminate immature females by piercing their integument. Among eSSD species, this behavior has been described only in *Latrodectus* (10) but may occur more widely.

Oral Sexual Encounters

Darwin's bark spider (*C. darwini*; SSD 2.6–3.9) performs cunnilingus-like oral sex (51). Field and laboratory studies imply that oral sexual encounters are obligatory, regardless of female mating and plug status (51). Further research will clarify this rare animal behavior and its relation to eSSD, if any, but it could plausibly be a signal, like mate binding, to reduce female aggression or perhaps to enhance paternity.

THE PERILS OF EXTREME SEXUAL SIZE DIMORPHISM

eSSD probably inflicts costs on giant females. The phylogenetic and taxonomic scatter of gigantism itself suggests that this rare phenomenon is confined to relatively distal clades, suggesting evolutionary instability, or that selection differentials rarely sum to cause its evolution. In this section, we explore potential pitfalls of eSSD for giant females to suggest new hypotheses. Perhaps eSSD, like extreme social behavior (3), is an evolutionary dead end.

Kleptoparasite Loads and Increased Predation

We hypothesize that the cost of kleptoparasites scales with the size of the host. Kleptoparasite numbers positively correlate with host web size (2). Large durable webs have many kleptoparasites, particularly in the tropics. Some kleptoparasites are flies (75), but most are small spiders, usually theridiids, that outnumber the host (1, 34). Although in some cases mutualism is also possible (115), kleptoparasitic spiders mostly steal prey and silk (136) and may even eat the host's eggs or the host herself (**Figure 4*h–j***). They are mainly a cost to large spiders.

Predation risk could either increase or decrease with increased body size. Perhaps giant females escape predators adapted to smaller prey. Even larger females could evolve, as may have happened in African *Trichonephila* (81, 86). However, larger females, simply by being more conspicuous, might increase attack rates by common predators and therefore mortality. Specific or general studies on how and why spiders die, whether or not they are giant females, are lacking.

Nutrient Deficiency

We hypothesize that giant females are limited by the quantity or quality of large prey available. Most spiders are generalist predators of arthropods. However, since giant females construct giant webs (**Figure 5*a–c***), they likely need more nutrition, possibly in different proportions (148). Balancing protein demands between growth and web construction may be problematic for web spiders (13). Some orb webs are optimized to subdue large, rare prey essential for growth and reproduction (12, 141). Large spiders occasionally eat vertebrates, as when giant female *Nephila*, *Trichonephila*, *Nephilingis*, and *Argiope* capture bats and birds (111). Widows (*Latrodectus*) disproportionately eat large ground-dwelling invertebrates, and sometimes vertebrates. *Caerostris* (**Figure 5*c***) apparently does not eat vertebrates, despite its giant web and exceptionally strong silk (48). The fishing spiders (*Dolomedes*) eat fish, particularly in the tropics (112), and large tropical wanderers (Ctenidae, Pisauridae, Theraphosidae) prey on frogs (102). All of these clades either are wholly eSSD or contain giant female species.

Web Functionality Limitations

We hypothesize that eSSD females may have reached a maximum size limited by functional constraints on hubs, radii, and spirals. Orb web architecture and function vary widely (12). In nephilids, small juvenile webs are round and symmetric, but older, larger instars spin increasingly asymmetric webs (85, 87). In *N. pilipes*, mass and hub displacement are strongly correlated (84). Gravity thus forces heavy spiders to make their webs asymmetric to maintain foraging efficiency success. Some giant female nephilid webs (*Nephilingis*, *Nephilengys*, and *Herennia*) are more ladder- than orb-like (86), with extreme hub displacement (**Figure 5*b***), indicating that these spiders have reached a maximum.

Selection for Sexually Dimorphic Body Shapes

We hypothesize that eSSD species have more pronounced sexual shape dimorphism. Orbweavers are commonly sexually dimorphic in color and morphology, not just size. In argiopines, body

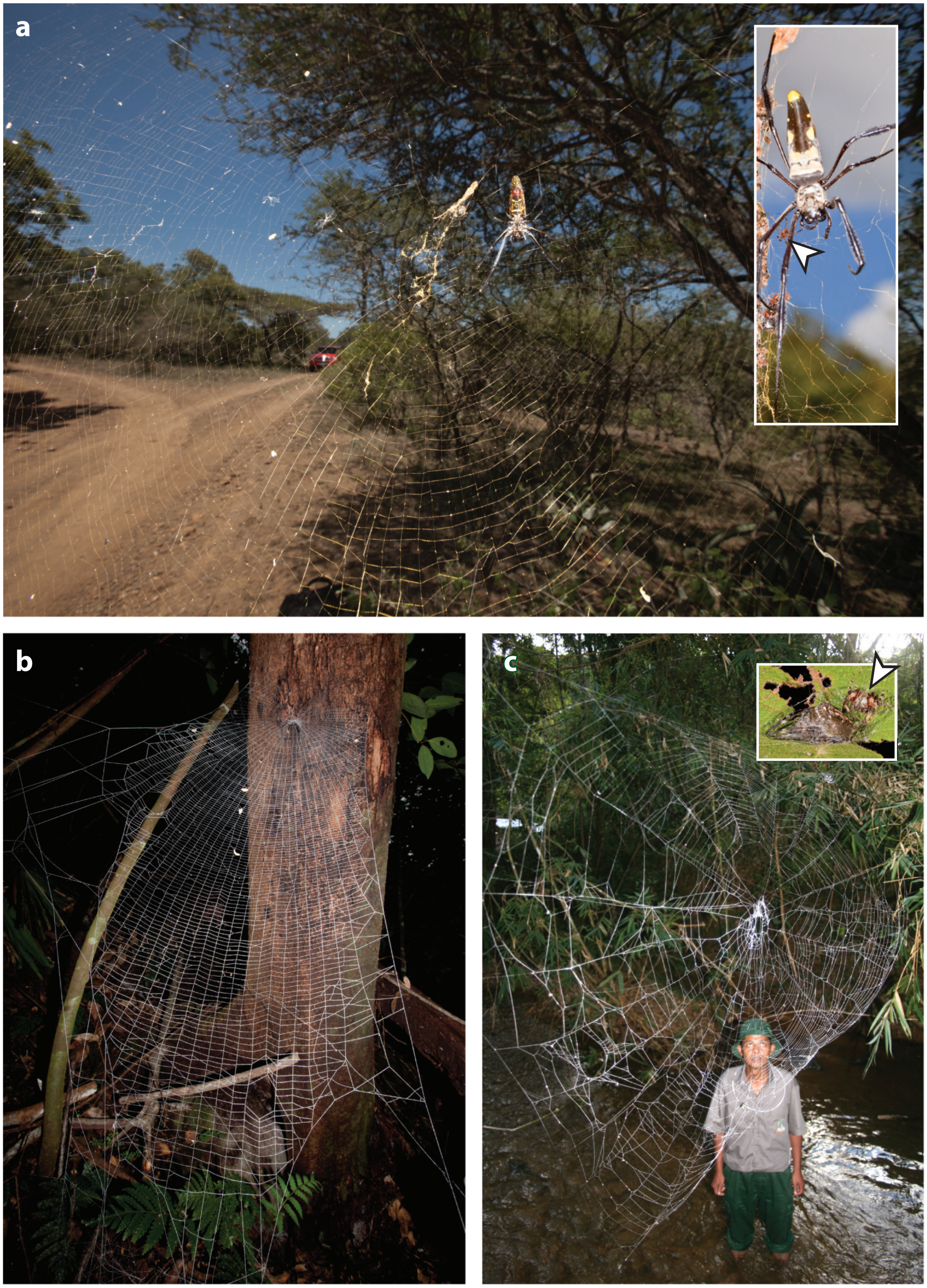


Figure 5

Web gigantism. (*a*) A typically huge golden orbweb of the South African *Trichonephila komaci*. (*b*) A giant ladder web of *Nephilingis livida*; this web in Seychelles measured over 1 m in height, and its hub was maximally displaced upwards. (*c*) Web of Darwin's bark spider (*Caerostris darwini*) in Madagascar. All of these species display extreme sexual size dimorphism (insets in panels *a*,*c*: arrows point to males). Image copyright M. Kuntner.

shape and SSD were unrelated, but at higher hierarchical levels, they were correlated phylogenetically, with extreme shape dimorphism being nested inside eSSD clades (24). If giant females experience more predation than smaller females, either ontogenetically or phylogenetically, then runaway evolution in female body shape could take place. Selection for increased shape dimorphism in SSD clades could result, especially if male and female phenotypes are weakly correlated. Araneids display particularly notable sexually dimorphic body shapes. Females mimic leaves, tree buds, bark, seeds, dirt, and bird droppings, and many have thorn-like abdominal projections (24). If such runaway selection is irreversible, and shape dimorphism incurs costs, then lineages could go extinct.

Genital Size Mismatches

We hypothesize that genital size mismatch can be a cost of eSSD. Under isometry, the difference in body size in giant female clades would pose genitalic difficulties. Genital mismatch should cause problems in mating. Indeed, two out of three theoretical models of SSD and sexual genital size dimorphism predict genital size mismatches (98, 122). In *T. edulis*, male genitalia and size are hypoallometric (138). Females are isometric, implying that selection optimized medium male genital size in spite of body size variation (138). If this is true, then the male intromittent organ has one particular optimal size in this species. A study that tested for genital size mismatch in nephilids found no correlations between SSD and sexual genital size dimorphism (98), thus nominally falsifying the three theoretical models. However, the male intromittent organ and the internal female genitalia sizes were independent of body size. Male intromittent and nonintromittent genitalic features and female external genitalia covaried (98), implying coevolution of genitalic structures that interact functionally. It seems that the genital mismatch peril of eSSD can be avoided via concerted evolution of male and female genital parts on the one hand and the independence of somatic and genital size evolution on the other.

Reproductive Interference

We hypothesize that reproductive interference can be a cost of eSSD. Increased SSD leads to male-biased operational sex ratios and intense male–male competition. Large males tend to win direct combats in orbweavers (105), with exceptions (71). If closely related species occur in close sympatry and without infallible premating isolation mechanisms, then heterospecific reproductive interference is possible (52). Nephilid males regularly court heterospecific females in their webs and may compete to guard them. A study of four African *Trichonephila* species (121) found that 20–60% of webs harbored the wrong species of males, who guarded the wrong females and competed among themselves and against heterospecific males. Heterospecific mating occurred but resulted in no offspring (121). Because *Trichonephila komaci* has significantly smaller (weaker) males than the other species studied, and is both rare and range restricted, the authors hypothesized that *T. komaci* experiences reproductive interference. This could potentially drive a species or a lineage to extinction.

Permanent Sperm Depletion

We hypothesize that permanent sperm depletion cannot be reversed. Male spiders have normal abdominal testes but store and transfer sperm in their palps. Unlike most other spiders, males of species with giant females like *Trichonephila*, *Nephilengys*, and *Tidarren* stop sperm production just before sexual maturity, and their testes atrophy, leading to permanent sperm depletion (103).

Sperm depletion is known to occur only in a handful of monogynous eSSD spiders. Unlike the former genera, and despite being monogynous, widows (*Latrodectus*) do not experience permanent sperm depletion (106). *T. senegalensis* reverts to polygyny, but only by rationing sperm within their one-shot genitalia (116, 129). Since one-shot genitalia can inseminate few females (129), and regaining sperm production might be impossible, permanent sperm depletion may ultimately drive a species or lineage to extinction.

CONCLUSIONS

eSSD is rare in gendered free-living organisms but is particularly well known in orbweaving spiders. eSSD animals tend to be small males living parasite-like lifestyles or large sedentary females with smaller motile males. If fecundity, but not mortality, increases with female size, then large female size should tend to evolve, but this cannot explain the lack of correlation with male size. We therefore adapt the differential equilibrium model to apply specifically to spider biology (**Figure 2**).

Most prior literature tested size-related predictions in selected model species, but we advocate more comparative phyletic approaches. Understanding of eSSD would be simpler but incorrect had only a handful of model species been used (83). Examination of whole clades with comparison of their macroevolutionary patterns, as well as experimental interrogation of the underlying selection pressures, allows for a more balanced evaluation of the differential equilibrium model. Although eSSD phenotypes in different spider clades seem comparable, if convergent, consideration of origins, proximate mechanisms, and eSSD biology suggests that they result from diverse pathways and selection pressures.

In isolation, none of the proposed hypotheses succeed in generally explaining the evolution of spider eSSD. Evidence remains equivocal for the differential mortality, gravity, sexual cannibalism, sperm, and scramble competition hypotheses, although these drivers may indeed explain some of the size variation. **Figure 1*c*** and **Supplemental Appendix 1** list the most prominent lineages that could constitute new tests. Alternative, untested hypotheses could explain female gigantism. Ability to spin giant webs may be a threshold above which predation is reduced. Sexually antagonistic coevolution could allow runaway selection for female gigantism.

Supplemental Material >

Extreme phenotypes that seem to be unusually common in eSSD spiders relate to mating opportunities, duration, and sperm competition for higher paternity. Sexual cannibalism, genital damage, and emasculation coevolve with eSSD. This eSSD mating syndrome may include other traits, but more work on function and phylogenetic pattern is needed.

Ultimately, eSSD may inflict high maintenance costs and in the long run may be an evolutionary dead end. This would explain its rarity among spiders and other similar (gendered, free-living, terrestrial) organisms. No known eSSD clades are notably species rich.

SUMMARY POINTS

1. SSD is not itself a trait under selection, but rather a phenotypic outcome of diverse, gender-specific directions of body size evolution.
2. Although most spiders are only moderately size dimorphic, some clades evolve extreme female-biased SSD values, termed eSSD in this review.
3. In isolation, fecundity, differential mortality, gravity, and sexual cannibalism do not fully explain eSSD.

4. Proposed drivers of SSD in spiders can be unified conceptually within the differential equilibrium model, but pathways and pressures will be clade, species, and context specific.
5. eSSD as a phenomenon is highly correlated with extreme sexual phenotypes, termed the eSSD mating syndrome in this review.
6. If, in the long run, the costs of female gigantism become very high, then eSSD may represent an evolutionary dead end.

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