

Sexual size dimorphism in spiders: patterns and processes

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7.1 Introduction

Spiders (Araneae) are known for the most spectacular cases of sexual size dimorphism (SSD) among terrestrial animals. In several species of web-building spiders females are giants compared to their tiny male counterparts and may outweigh them by more than 100 times (Head 1995; Vollrath 1998). The evolution of such extreme SSD has puzzled researchers since Darwin (Darwin 1871; Gerhardt 1924; Elgar 1992; Vollrath and Parker 1992; Andersson 1994; Head 1995; Coddington *et al.* 1997). In fact, its evolutionary significance is far from resolved and remains controversial (e.g. Vollrath and Parker 1992; Coddington *et al.* 1997; Prenter *et al.* 1998, 1999; Moya-Laraño *et al.* 2002a, 2005a, 2005b). Apart from the most extravagant cases, spiders exhibit the whole range of SSD, from extreme female-biased to male-biased, with females being larger than males in the majority of species (Head 1995; Vollrath 1998). Interestingly, both male-biased SSD and extreme female-biased SSD occur in several distinct spider taxa, and extreme SSD has evolved several times independently, even within the orb-web spiders (Hormiga *et al.* 2000). Spiders are the only terrestrial animal taxon that exhibits such a broad range of SSD and in which extreme SSD is relatively common (Ghiselin 1974; Andersson 1994). Hence, spiders offer a unique and tangible system to study the ultimate and proximate factors that drive the evolution of SSD. In this chapter, we first clarify important issues regarding spider morphology as they relate to size dimorphism and then elucidate

the patterns of SSD within the spiders. Finally, we present the hypotheses for the adaptive significance of SSD in spiders as well as the current evidence for and against these and emphasize areas for future research.

7.2 Spider morphology: dimorphism in size and shape

Spiders have two major body parts, the anterior prosoma and the posterior opisthosoma (Figure 7.1). The prosoma is a cephalothorax and encompasses the head region with eyes, fangs, and pedipalps, plus the thorax region to which the four pairs of walking legs are attached. The opisthosoma is the spider's abdomen containing most of the visceral organs, the gonads, and the silk glands (Foelix 1996). To understand spider size it is important to consider the pattern of growth in spiders. As arthropods, spiders undergo a series of molts during the ontogeny, shedding their cuticle in each of the molts (Foelix 1996). The prosoma and legs grow only during a molt when liquefied reserves from the abdomen are pumped into the anterior regions of the body to expand the new and still soft cuticle (Foelix 1996). The vast majority of spider species exhibit determinant growth and do not molt after maturity (Foelix 1996). Thus, prosoma and leg traits are frequently referred to as fixed traits. Prosoma traits, such as carapace width, are typically highly correlated with body mass at maturation (Foelix 1996) and are therefore very useful and easy to measure for estimating a spider's size. On the other hand, the abdomen's

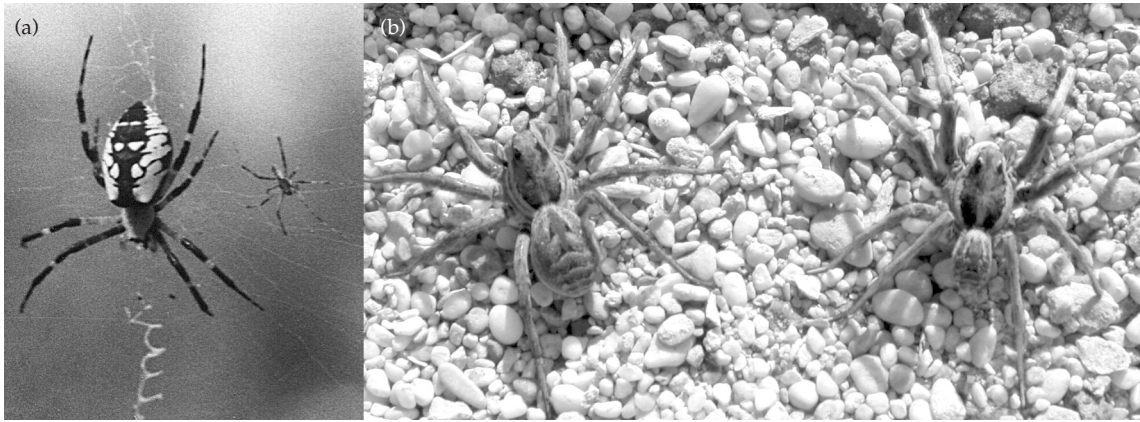


Figure 7.1 (a) A female (left) and a male of the orb-web spider *Argiope aurantia*, a species with extreme SSD. (b) A female (left) and a male of the wolf spider *Lycosa tarantula*, a species with little SSD. Note that panels a and b are not to the same scale. (a) M. Foellmer Photo credit: (b) E. de Mas.

cuticle is flexible. Its dimensions change with changing body mass as a function of foraging success and reproductive state (e.g. female egg load) and are thus condition-dependent (Prenter *et al.* 1995; Moya-Laraño 2002). Adult males in many species do not feed and hence their abdomen shrinks over time as reserves are used up (e.g. Foellmer and Fairbairn 2005b). The same also applies to body length, which depends partly on abdomen length. Hence, body-mass and abdomen traits are commonly employed in indices of body condition (e.g. Moya-Laraño 2002; Moya-Laraño *et al.* 2003; Foellmer and Fairbairn 2005a, 2005b).

In many spider species, if not all, the sexes typically differ not only in size, but also in shape; that is, in the relative size of body parts (e.g. Prenter *et al.* 1995). Males have relatively longer legs than females, and in males, but not females, legs exhibit a positive allometric relationship with carapace width (Eberhard *et al.* 1998; but see Uhl *et al.* 2004). Leg length as a size trait will thus often underestimate SSD and should only be used in combination with carapace width in multivariate selection studies to discern selection on body size and body-size components (Foellmer and Fairbairn 2004, 2005a, 2005b). Little is known about sex-specific investment in the prosoma compared with the abdomen at maturation, which warrants further study. We thus recommend using carapace width as a standard size trait for spiders along with other relevant traits to capture shape and condition.

7.3 The pattern of SSD in spiders

Although in most spider species females are the larger sex, there is great variation in SSD across species (e.g. Head 1995; Vollrath 1998). Extreme SSD occurs mostly in, but is not limited to, the Orbiculariae (orb-web spiders) and Thomisidae (crab spiders), where females may weigh 100 times as much as males or, when expressed on a linear scale, be about five times as long, and these are not even the upper limits (Head 1995; Vollrath 1998; Hormiga *et al.* 2000). The evolution and coevolution of male and female body size in spiders are still not fully understood. Of interest are two questions: (1) do spiders exhibit interspecific body-size allometry consistent or inconsistent with Rensch's rule (see Chapters 1 and 6 in this volume)?; (2) is the evolution of body size in the sexes uncoupled? Answers to these questions may well turn out to be different for different spider groups and are essential for testing hypotheses about selection processes that drive the evolution of SSD within the Araneae. Rensch's rule posits that within a clade males evolve to a large size at a faster rate than females, and that this is manifested in an allometric trend: SSD increases with mean size in taxa in which males are the larger sex, and decreases in those in which females are larger (Fairbairn 1997). Rensch's rule is prominent but not universal in the animal kingdom (Abouheif and Fairbairn 1997; Chapter 6 in this volume). The

second question addresses the extent to which the sexes evolve in the same direction. In most animal taxa, male and female body sizes are highly correlated, suggesting tight coevolution (Fairbairn 1997).

Abouheif and Fairbairn (1997) and Fairbairn (1997) suggested that spiders do not exhibit body-size allometry consistent with Rensch's rule, and that the correlation between male and female size may be lower in spiders than in most other animal taxa, indicating relatively uncoupled evolution of their sizes. Other comparative studies also suggested that SSD in spiders increases with increasing female size and that it depends little on male size, supporting the notion that females have diverged more in size over evolutionary time (Head 1995; Prenter *et al.* 1998, 1999). A phylogenetic analysis of the Orbiculariae showed that extreme SSD has evolved several times independently and that this has involved different evolutionary pathways (Hormiga *et al.* 2000). Increases in female size contributed most to SSD evolution, and SSD has even been lost in some lineages. Taken together, these results suggest that, overall, changes in female size have been more important for generating current SSD in spiders than changes in male size.

Almost all studies and claims about the pattern of SSD in spiders have been based on body-length data taken from identification manuals and similar literature (Vollrath and Parker 1992; Head 1995; Abouheif and Fairbairn 1997; Coddington *et al.* 1997; Prenter *et al.* 1997, 1998; Hormiga *et al.* 2000; but see Prenter *et al.* 1999). As stated in section 7.2, this may entail problems because body length is confounded with condition. Thus, in comparative analyses of the evolutionary divergence of male and female size the use of body length might lead to wrong conclusions due to the introduction of considerable error in the detection of evolutionary trends. Prenter *et al.* (1999) used carapace width in their comparative analysis and could confirm some of the results obtained in other studies. However, the problem remains that for interspecific comparisons most of the literature considers only body-length data.

Here we present an updated evaluation of the distribution of SSD and its allometry in

spiders and examine specifically whether and to what extent the interpretation of results differs depending on the body-size measure used (body length compared with carapace width). We further examine whether body-size allometry differs between two large spider clades for which we have data, the Orbiculariae and the RTA clade (Coddington 2005). The Orbiculariae comprise orb-web spiders and derived web-weavers and include most of the spider species with extreme SSD (Hormiga *et al.* 2000). Most taxa in the RTA clade do not build prey-catching webs, and with the exception of some crab spiders (LeGrand and Morse 2000) most species show little dimorphism (for methods see Box 7.1).

The SSD estimates based on body length (BL) and those based on carapace width (CW) not surprisingly are correlated significantly (Spearman's rank correlation coefficient, 0.648, $P < 0.001$), but there is considerable scatter (Figure 7.2). SSD based on body length is significantly larger than SSD based on carapace width (Figures 7.2 and 7.3): for SDI-BL mean = 0.29, median = 0.23, range = -0.07 to 3.52; for SDI-CW mean = 0.11, median = 0.08, range = -0.52 to 3.09 (Wilcoxon signed ranks test, $Z = -18.04$, $P < 0.001$). The discrepancy between the two size measurements likely reflects the fact that body length is confounded by condition, especially by female egg load. Additionally, it is possible that body length as a trait is more dimorphic than carapace width independent of condition. Nevertheless, females are larger in most species regardless of which size estimator is used.

Figure 7.3 summarizes SSD for our sample by taxonomic category. The most extreme cases of SSD are found within the Araneidae. Note that some prominent families such as the sheet-web weavers (Linyphiidae), which contain probably many species with larger males (Lang 2001), are not included in our sample, because they are not covered in the books we used as our data sources. For other family-level summaries of SSD in spiders based on body length see Prenter *et al.* (1997, 1998) and Vollrath (1998).

The use of body length or carapace width has relatively little effect on estimates of body-size allometry (Table 7.1). The major-axis regression slopes are essentially identical when all species are

Box 7.1 A comparative analysis of the pattern of SSD in spiders

Data were taken from identification manuals published in the series *The Insects and Arachnids of Canada* (Dondale and Redner 1978, 1982, 1990; Platnick and Dondale 1992; Dondale *et al.* 2003), which for each species provides data for both body length and carapace width. Thus we base our analysis on species from a large and diverse geographical area. We used the updated species classification following the World Spider Catalog (version 6.5; <http://research.amnh.org/entomology/spiders/catalog/INTRO1.html>). A total of 489 species from 15 families and 86 genera were included in the analyses. As an index of SSD we used the size dimorphism index (SDI; Lovich and Gibbons 1992). The SDI is calculated as the larger sex divided by the smaller sex minus 1, arbitrarily set to negative when males are larger. To evaluate body-size allometry we followed the standard approach and present the results both for \log_{10} -transformed species data, not corrected for phylogeny (so-called tips), and for phylogenetically independent contrasts (Fairbairn 1997). Independent-contrast analysis corrects for similarity between species that is due to common ancestry (reviewed in Garland *et al.* 2005). We

used PDAP version 6.0 (Garland *et al.* 2005) to calculate independent contrasts based on the current knowledge of spider phylogeny (Coddington 2005, Murphy *et al.* 2006). Unresolved nodes were entered as polytomies, so taxonomy was assumed to reflect phylogeny. That is, if no other information was available, all genera descended from the common family node and all species from the common genus node. In the absence of estimates for branch lengths we set all branch lengths arbitrarily equal to 1, and diagnostic methods (Garland *et al.* 2005) did not reveal any problem with our branch lengths. Independent-contrast analysis has been shown to be robust in case of incomplete phylogenies (Garland *et al.* 2005).

We used model II (major-axis) regression to estimate the allometric slope of $\log(\text{male size})$ on $\log(\text{female size})$, since both variables can be expected to have similar measurement errors and the assignment to axis is arbitrary (Fairbairn 1997). The corresponding regression for independent contrasts was forced through the origin (Garland *et al.* 2005). A slope > 1 indicates allometry consistent with Rensch's rule.

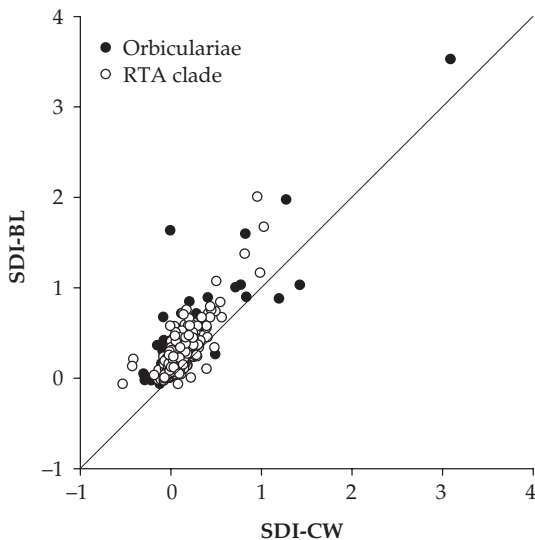


Figure 7.2 The relationship between SSD (calculated as the Lovich and Gibbons (1992) size dimorphism index; see text) based on body length as a size measurement (SDI-BL) and SSD based on carapace width (SDI-CW). Data points are shown for the two spider clades. The diagonal line depicts the line of equality between the two indices.

combined and within the RTA clade. A slight difference is noticeable for the Orbiculariae. The lower orbicularian body-length tips slope is likely the result of gravid females being included, but this disappears when independent contrasts are considered. This result can be seen as comforting: the measure provided in most identification manuals can be used without the danger of bias. The slopes for the uncorrected species tips data are all < 1 , and two of them significantly so (all spiders combined and the RTA clade based on carapace width) as judged by their 95% confidence intervals not encompassing 1 (Table 7.1, Figure 7.4). Orbiculariae show greater scatter, so their confidence interval overlaps 1 (Table 7.1, Figure 7.4). Independent-contrast analyses generally confirm the slopes based on uncorrected tips data in our data-set, although none is significantly different from a slope of 1. Interestingly, the Orbiculariae and the RTA clade do not differ with respect to the independent-contrast regression slopes. Thus, spiders do not show SSD allometry consistent with

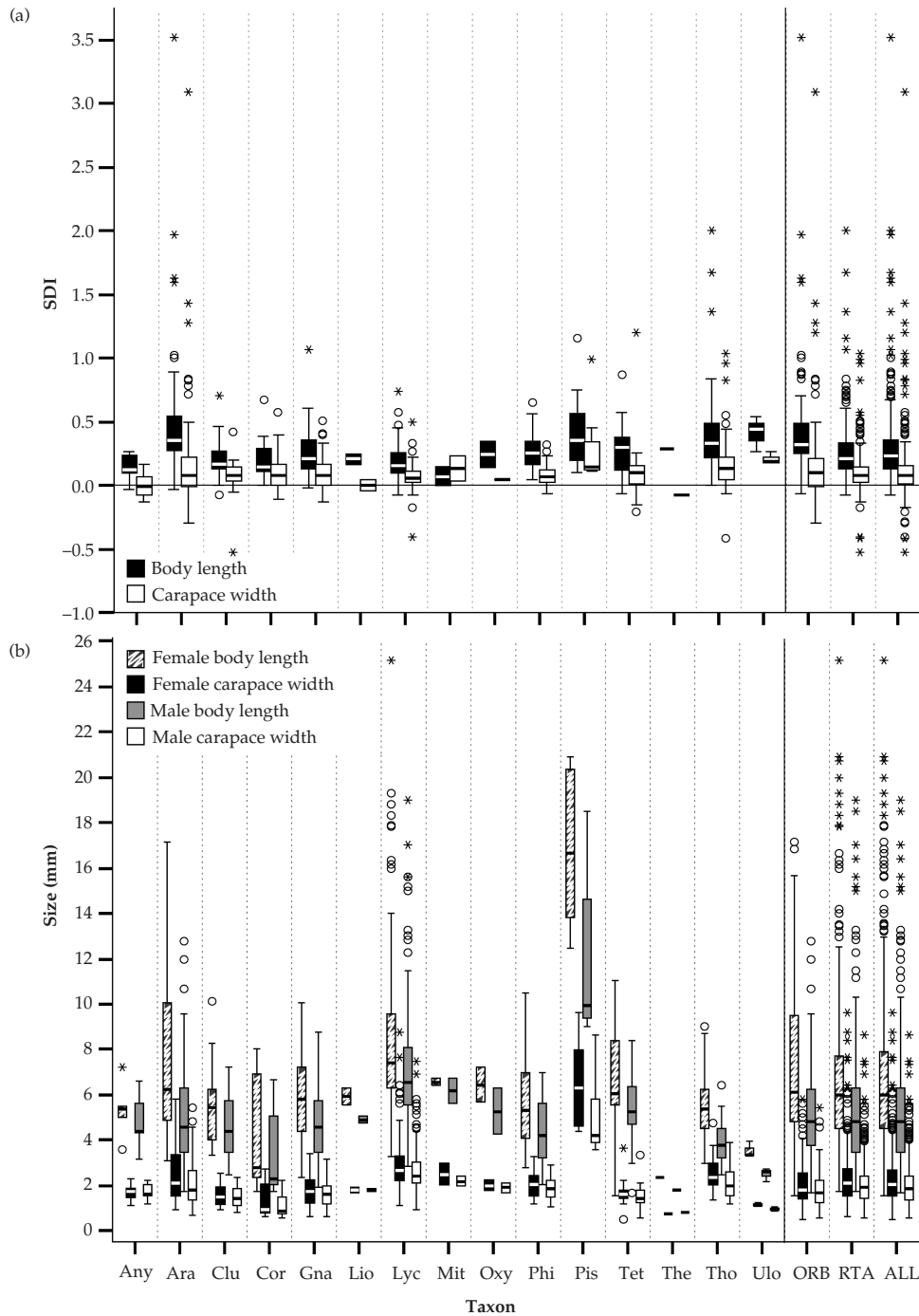


Figure 7.3 (a) Box plots for the distributions of SDI based on body length and carapace width. The horizontal reference line indicates no dimorphism (SDI = 0). (b) Box plots for the distributions of body length and carapace width for males and females. Taxonomic categories are the families included in our analysis as well as the RTA clade, the Orbiculariae, and all species combined. Horizontal lines within boxes are the medians; lower and upper box limits are the 25th and 75th percentiles respectively. Circles depict outliers that are 1.5–3 box lengths (i.e. interquartile ranges) from the end of the boxes; asterisks show extreme values (> 3 box lengths). Any, Anyphaenidae; Ara, Araneidae; Clu, Clubionidae; Cor, Corinnidae; Gna, Gnaphosidae; Lio, Liocranidae; Lyc, Lycosidae; Mit, Miturgidae; Oxy, Oxyopidae; Phi, Philodromidae; Pis, Pisauridae; Tet, Tetragnathidae; Tho, Theridiosomatidae; Tho, Thomisidae; Ulo, Uloboridae; ORB, Orbiculariae; RTA, RTA clade; ALL, all species combined.

Table 7.1 Major-axis regression slopes for log(male size) on log(female size) for all spiders combined and for the Orbiculariae and the RTA clade separately. Also given are the Pearson correlation coefficients, r . Size is either based on body length (BL) or carapace width (CW). Tips, regression based on log-transformed species data; ICs, regression based on phylogenetically independent contrasts.

			<i>N</i>	MA slope	95% CI	MA intercept	<i>r</i>
All species	BL	Tips	489	0.96	0.04	-0.07	0.92
		ICs	152	0.96	0.11		0.86
	CW	Tips	489	0.96	0.03	-0.03	0.94
		ICs	152	0.95	0.10		0.87
RTA clade	BL	Tips	396	0.98	0.04	-0.08	0.94
		ICs	97	0.98	0.14		0.86
	CW	Tips	396	0.96	0.03	-0.03	0.97
		ICs	97	0.96	0.11		0.90
Orbiculariae	BL	Tips	93	0.87	0.14	-0.04	0.85
		ICs	54	0.93	0.20		0.85
	CW	Tips	93	0.95	0.15	-0.04	0.85
		ICs	54	0.92	0.23		0.81

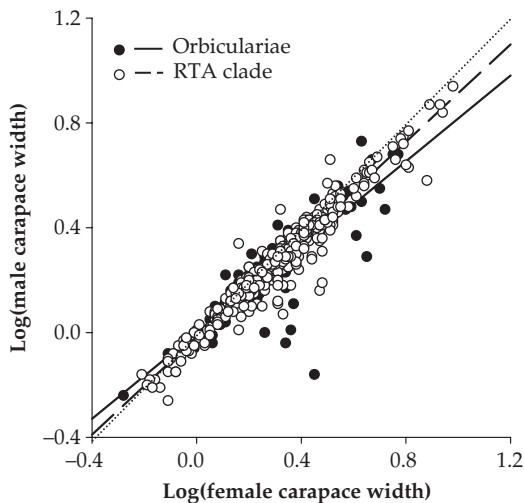


Figure 7.4 The relationship between log (male carapace width) and log(female carapace width) for the Orbiculariae and the RTA clade. The dotted line depicts a slope of 1. Also shown are the least-squares regression lines. For major-axis regression results see text and Table 7.1.

Rensch's rule; instead, females appear to have diverged more in size over evolutionary time, conforming to previous interpretations (Fairbairn 1997; Prenter *et al.* 1999).

Conspicuous are the relatively low Pearson correlation coefficients for the independent contrasts

(Table 7.1). Figure 7.4 illustrates the scatter; that is, the relatively low correlation between male and female size. This suggests that male and female body size can indeed evolve in a relatively uncoupled fashion in some species, especially in orb-weavers, which is truly unusual for animals (Fairbairn 1997). Below we discuss possible reasons for this. Future studies should also focus on single subgroups such as families to investigate when and why the evolution of male and female body size is decoupled. On a proximate level, such uncorrelated changes in body size between the sexes are probably mediated by an asynchronous change in the number of instars, combined with adjustment of growth rates to ensure timely maturation in seasonal habitats (Higgins 2002; Blanckenhorn *et al.* 2007). Spiders are known for their high inter- and intraspecific variability in instar number (e.g. Hallas 1989). Possible constraints limiting the evolution of SSD still need to be identified. For instance, there is a great need for quantitative genetic studies of sex-specific growth strategies in spiders (Uhl *et al.* 2004). A recent study revealed that SSD can have an impact on the mating system of a species and that SSD may be constrained by genital mechanics (Ramos *et al.* 2005). In species with extreme female-biased SSD the female genitalia are larger relative to male

genitalia than in species with moderate or no SSD. This should facilitate multiple mating by females, because mating with several males may be necessary to fill the female's spermathecae (Ramos *et al.* 2005). At the same time, the relationship between SSD and genital dimorphism possibly sets limits to the evolution of extreme SSD if the sexes cannot evolve apart in size beyond a necessary genital match (Ramos *et al.* 2005). This point is illustrated by the highly dimorphic cob-web spider genus *Tidarren*, in which the tiny males voluntarily remove one of their relatively large pedipalps prior to maturation, which greatly improves their locomotory performance and endurance (Ramos *et al.* 2004), demonstrating also how selection has favored male strategies that increase the probability of reaching females (see below).

7.4 Hypotheses for the adaptive significance of SSD in spiders

Until the maturation molt, males and females of a given spider species have very similar lifestyles (e.g. building prey-catching webs). Invariably, and even in actively hunting spiders (Persons 1999; Moya-Laraño *et al.* 2002a), males are the searching sex, which upon maturation change lifestyles considerably and stop building prey-catching webs or even feeding (Foelix 1996; Foellmer and Fairbairn 2005b). Hence, most of the adaptive hypotheses for the evolution of SSD in spiders focus on male agility or the ability to find a receptive female. Below we review sex-specific patterns of selection in spiders as they pertain to the evolution and maintenance of SSD.

7.4.1 Selection on female body size

There is good evidence that fecundity selection favoring large size in females is a major factor contributing to the evolution and maintenance of SSD in spiders. Female size correlates positively with clutch size in spiders, both at the inter- and intraspecific level (Marshall and Gittleman 1994; Head 1995; Prenter *et al.* 1999; Higgins 2002). Further, SSD correlates positively with female body size and clutch size (Head 1995; Prenter *et al.* 1998, 1999).

However, the relationship between female size and reproductive success is more complex because female lifetime reproductive success depends not only on clutch size, but also on clutch number and fertility (Higgins 2000, 2002; Roff 2002). Adding an instar greatly increases clutch size (Higgins 2002) but also prolongs development time, which may translate into higher cumulative juvenile mortality, less time for reproduction in a seasonal environment (Higgins 2000; Roff 2002), and potentially mate limitation (Higgins 2000; Moya-Laraño *et al.* 2003). Hence, if being large and maturing early is strongly favored, then in turn selection should favor fast growth and efficient resource-acquisition abilities (Higgins 2000; Blanckenhorn *et al.* 2007), balanced by increased mortality as a result of voracious but risky foraging (Arnqvist and Henriksson 1997; Higgins and Rankin 2000). The relative importance of these factors and the trade-offs involved are still poorly understood in spiders.

It has also been hypothesized that large size is favored in females because they may outgrow their predators (Hormiga *et al.* 2000; Higgins 2002). For this hypothesis to hold, it remains to be demonstrated that the cost imposed by voraciousness on juvenile mortality is outweighed by substantially lower mortality of larger adult females.

Which factors contribute to the large inter-specific variation in female body size is not well known. Why have females in some spider species grown into giants, while females in others have not (Hormiga *et al.* 2000)? It has been argued that differences in prey availability (i.e. habitat productivity), habitat structure, foraging mode, and phenology are important constraints on the fecundity benefits of large size and thus determine the reproductive schedule and output (Enders 1976; Craig 1987; Head 1995). An interesting example of probable physiological and ecological constraints on female size is provided by the aquatic spider *Argyroneta aquatica*. In this species, females are smaller than males. Females have to collect air more frequently than males and appear to be limited by the costs of building air bells, the size of which is correlated with female body size (Schütz and Taborsky 2003).

7.4.2 Selection on male body size

We discuss a number of non-exclusive hypotheses for the adaptive significance of small male size in spiders. All major hypotheses are based on one or more of the following premises: (1) when population densities are low, selection for large size by male–male interference competition is relaxed; (2) in general, but most importantly when population densities are low, receptive females are scattered, thus limiting resources, and selection must favor those male morphologies or strategies that are better for reaching females and confer an advantage either in scramble competition or in anti-predatory behavior; and (3) females may impose direct selection on male size via either sexual cannibalism or mate choice.

The sexual-cannibalism hypothesis

Sexual cannibalism is relatively common in spiders (Elgar 1992). The original sexual-cannibalism hypothesis tried to explain the evolution and maintenance of extreme female-biased SSD (Darwin 1871). According to this hypothesis, small males have an advantage because they may be more agile and thus faster at escaping female attacks, or may fall below a presumed threshold above which females can detect approaching males or consider them valuable prey (Darwin 1871; Elgar 1992). This hypothesis has been refuted in all direct and indirect tests conducted to date in highly dimorphic species (reviewed in Foellmer and Fairbairn 2004; but see Elgar and Fahey 1996), and in less dimorphic species larger males are actually better at escaping female attacks (e.g. Persons and Uetz 2005; reviewed in Foellmer and Fairbairn 2004).

Hypotheses based on low population densities and/or early maturation

The next three hypotheses trying to explain extreme SSD in spiders are based on related assumptions. The protandry hypothesis posits that maturing earlier than females is adaptive for males because males that mate first with a female will sire most or all of her offspring (Morbey and Ydenberg 2001). This should lead to female-biased SSD assuming a positive correlation between development time and adult size (Roff 2002). In most spider species males

indeed mature earlier than females (Jackson 1986; Maklakov *et al.* 2004). The Ghiselin–Reiss hypothesis (Ghiselin 1974; Reiss 1989) posits that in species living at low densities the probability of males congregating around receptive females is so low that male–male interference competition is relaxed, thus conferring no advantage to larger males (Andersson 1994). Selection by scramble competition to reach females would then favor a morphology adapted for mate-searching and early maturation at a smaller size to increase the probability of survival to adulthood (Ghiselin 1974; Andersson 1994). The differential mortality model (Vollrath and Parker 1992) is also based on the assumptions of low densities and early maturation. However, in this model the lower densities only pertain to males of sedentary spiders. This hypothesis states that in species in which females stay relatively sedentary throughout their life (e.g. web-builders and crab spiders), males suffer from higher (size-independent) mortality than females during mate search, as compared to actively hunting species in which male and female mortality would be similar (Vollrath and Parker 1992). This would relax male–male interference competition in sedentary species and in turn viability selection would favor reduced growth and early maturation at male small size to increase the number of males reaching females.

Protandry could confer an advantage to males if females are not overly choosy (Maklakov *et al.* 2004) or if male interference competition were truly uncommon. Whereas in several spider species females appear to mate indiscriminately with respect to male body size (e.g. Kotiaho *et al.* 1996; Maklakov *et al.* 2004), in many other species, ranging from species with male-biased SSD to orb-weavers with extreme female-biased SSD, male–male interference competition is common and probably favors larger males because of their advantage in direct combat (reviewed in Foellmer and Fairbairn 2005a). Thus, the assumption of relaxation of male–male interference competition seems not to hold in many cases. In addition, females in many species mate multiply, and recent evidence suggests that sperm mixing is the most common pattern of sperm use by females (e.g. Schneider *et al.* 2000), although males may guard or plug females to prevent other males from mating (Cohn *et al.* 1988; Foellmer and

Fairbairn 2003; Fromhage and Schneider 2006). No study has yet attempted to demonstrate the adaptive significance of protandry in spiders, which requires showing that early-maturing males indeed have higher reproductive success (del Castillo and Núñez-Farfán 1999).

The Ghiselin–Reiss hypothesis predicts that small male size may also be favored in scramble competition if adult males have to feed regularly to maintain stamina, because lower metabolic requirements enable small males to spend more of their time and energy searching for females and mating (Reiss 1989; Blanckenhorn 2000). However, in most spider species adult males rely largely on energy reserves and rarely feed (Foellmer and Fairbairn 2005b). In such species large males may actually have an energetic advantage because of their lower mass-specific metabolic rate, or if energy-storing capacity scales hyper-allometrically with size (Calder 1984). Foellmer and Fairbairn (2005b) did not find a size-dependent energetic advantage in *Argiope aurantia*, a species in which adult males do not feed. Such an effect has yet to be demonstrated. The highly dimorphic crab spider *Misumena vatia* seems to fit the Ghiselin–Reiss hypothesis (LeGrand and Morse 2000). Population densities are low, males feed regularly, do not engage in fights over females, and can mate with several females (LeGrand and Morse 2000; Anderson and Morse 2001). Also, in species of the orb-weaver genus *Metepeira*, males are relatively smaller than females in populations of lower densities (Piel 1996).

There is major lack of support for the differential-mortality hypothesis, which predicts that sit-and-wait predators exhibit more pronounced female-biased SSD than active hunters and assumes a stage-dependent mortality difference between males and females (Prenter *et al.* 1997, 1998; Moya-Laraño *et al.* 2002a, Walker and Rypstra 2003). However, male mortality during mate search has been suggested to be high (approximately 80%) in some highly dimorphic web-building spiders (e.g. Andrade 2003). More studies are needed to elucidate whether high travel mortality is common in other spiders as well and whether it can balance sexual selection for large size due to interference competition.

The gravity hypothesis

The gravity hypothesis (Moya-Laraño *et al.* 2002a) posits that in species in which females live in high places where males must climb to reach them, males will be selected to be small, either because they have an advantage in scramble competition by reaching females faster or because they escape predators more efficiently while moving on vertical surfaces. Due to the constraint imposed by gravity, a simple biomechanical model based on physical first principles shows how, all other things being equal, the speed at which an animal can climb (v) is inversely proportional to its body length (L) or body mass (M). Relevant data are available for two highly dimorphic orb-weavers. In *Nephila clavipes*, in which females live in high to very high places, smaller males were more likely to reach females (Linn 2001). However, in *A. aurantia* large male size was actually favored in one of two populations (Foellmer and Fairbairn 2005b). This apparent paradox might be explained by the complex empirical relationship found between climbing speed and body size in spiders, which we now investigate here.

We conducted an experiment to investigate whether an animal shaped like a spider exhibits a negative relationship between climbing speed and body size, as predicted by the gravity hypothesis (J. Moya-Laraño, M. Foellmer, and C. Allard, unpublished work). Using a large body-mass range of spiders of different instars (0.2–881.4 mg) and phylogenetic affiliation we found surprisingly that the empirical relationship between body size and climbing speed is not purely negative but curvilinear (Figure 7.5), with an optimal body size for climbing at approximately 42.5 mg (approximately 7.6 mm; Edwards 1996), beyond which the negative relationship predicted by the gravity hypothesis arises. This may explain why Foellmer and Fairbairn (2005b) found positive directional selection on male body size during mate search in *A. aurantia*, as males weigh only approximately 20 mg.

Furthermore, we found a curvilinear pattern of SSD ($\log(\text{male body length})$ against $\log(\text{female body length})$) in spiders that live in habitats high off the ground and a linear pattern in spiders that live at ground level for the data-set of Moya-Laraño *et al.* (2002a). The pattern of SSD is

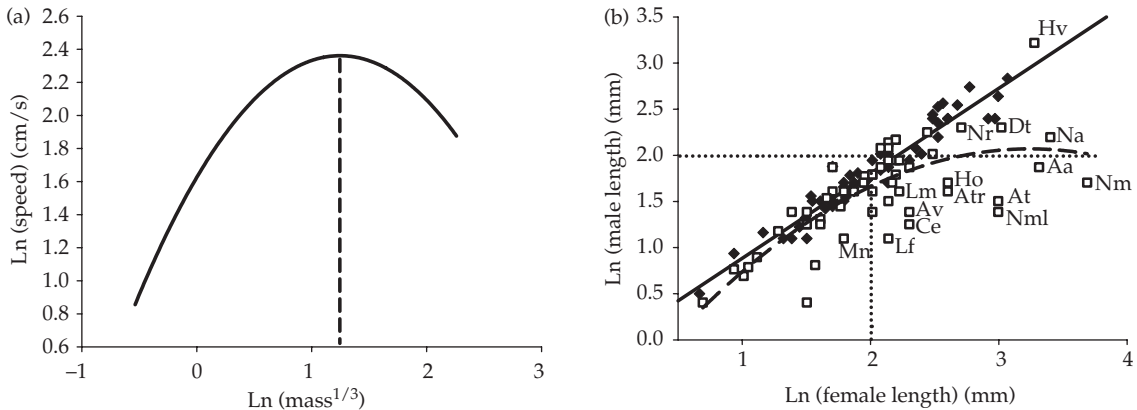


Figure 7.5 Empirical test of the gravity hypothesis and the influence of the (curvilinear) pattern on spider SSD. (a) Relationship between body size ($\ln(\text{mass})$) and $\ln(\text{climbing speed})$ in spiders of variable instars. The fitted curve is: $\ln(\text{speed}) = 1.63 + 1.18 \cdot \ln(\text{mass})^{1/3} - 0.05 \cdot \ln(\text{mass})^{1/3}^2$. Both the linear and quadratic mass terms are significant. The dashed vertical line shows the optimal body mass for climbing (approximately 42.5 mg). This relationship predicts a curvilinear pattern of SSD in spiders from habitats located high off the ground. (b) A plot of $\ln(\text{male size}) - \ln(\text{female size})$ (as used throughout this book) for spiders living at or close to ground level (low habitats; \blacklozenge , solid line) and high above ground level (high habitats; \square , dashed line). The horizontal and vertical dotted lines show the male and female body lengths respectively, which correspond to the optimal climbing speed (approximately 7.6 mm) extrapolated from (a). Note how in high-habitat spiders the curvilinear trend starts very close to the female threshold, as would be predicted by the pattern of climbing speed, and how beyond this threshold for all species but one (Hv) male sizes fluctuate around the threshold (horizontal dotted line). The linear (least-squares) model for low-habitat spiders is: $\ln(\text{male body length}) = 0.92 \cdot \ln(\text{female body length})$ ($P < 0.0001$). The curvilinear model for high-habitat spiders is: $-0.72 + 1.72 \cdot \ln(\text{mass}) - 0.27 \cdot \ln(\text{mass})^2$ (both the linear and quadratic mass terms were significant). Note that spiders from distant taxa are responsible for the curvilinear pattern: Araneidae (Aa, *Argiope aemula*; At, *A. trifasciata*; Atr, *Araneus trifolius*; Av, *A. versicolor*; Ce, *Cyrtophora exanthematica*; Nr, *Neoscona rufofemorata*), Nephilinae (Ho, *Herennia ornatissima*; Lf, *Leucauge fastigiata*; Na, *Nephila antipodiana*; Nm, *N. maculata*; Nml, *N. malabarensis*), Pisauridae (Dt, *Dolomedes tenebrosus*), Theridiidae (Lm, *Latrodectus mactans*), Thomisidae (Mn, *Misumenops nepenthicola*), and that there is one clear outlier (Hv, *Heteropoda venatoria*) which, like all Sparassidae, has a very flat body, lateral legs and abundant fine hair (*scopulae*), suggesting that this species may be highly adapted to climb.

linear in both spider groups up to the 7.6-mm threshold for female body size (the x axis), beyond which the correlation between male and female body size vanishes for high-habitat spiders, although it remains in ground-dwelling spiders (Figure 7.5). Thus, the concave relationship between male and female body size (Figure 7.5b) suggests that SSD in spiders living in high habitats is indeed mediated by male climbing ability. Our analyses therefore support the gravity hypotheses and also explain the lack of support for the hypothesis in some instances (Foellmer and Fairbairn 2005b). Furthermore, the gravity hypothesis provides an explanation for why male and female size are uncoupled in large orbicularians. However, climbing is not the only kind of movement necessary for spider males when females live in tall places. Males in this context have to also walk (or run) horizontally, bridge (walk upside-down from one branch to another using a

silk strand), and drop (from a higher to a lower place using a silk strand), and all these different types of movement should affect an optimal male body size.

Copulatory and post-copulatory processes

There is evidence for additional factors that could affect the evolution of SSD in the context of mating. In the highly dimorphic orb-weaver *Nephila edulis*, small males have been shown to employ a more efficient mating tactic in the absence of (large) competitors that confers a fertilization advantage (Schneider *et al.* 2000). However, larger males often prevent smaller ones from mating in *N. edulis*, which might help explain the large variability in male size in this species (Schneider and Elgar 2005).

7.4.3 The adaptive significance of SSD: integrating male and female effects

It is important to remember that it is the difference in net selection on size between males and females that

will ultimately determine SSD (the differential equilibrium hypothesis of SSD; Blanckenhorn 2000; Preziosi and Fairbairn 2000; Chapters 1, 9, and 10). Net selection is the sum of all effects during all relevant selection episodes (Arnold and Wade 1984b). Such data do not exist for any spider species so far and will be very difficult to obtain (Foellmer and Fairbairn 2005a). In most cases data are available for either females or males (e.g. Higgins 2002; Foellmer and Fairbairn 2005a). One exception is the burrowing wolf spider *Lycosa tarantula*. In spite of its moderate to low SSD (based on carapace width), selection acts quite differently on adult males and females. Whereas large carapace width confers higher male mating success (C. Fernández-Montraveta and J. Moya-Laraño, unpublished work), small carapace width confers lower mating success in females (Moya-Laraño *et al.* 2003) but favors females in fights over burrows and territories (Fernández-Montraveta and Ortega 1993; Moya-Laraño *et al.* 2002b). That is, body size seems to be under directional selection in males but under net stabilizing selection from opposing selective forces (*sensu* Preziosi and Fairbairn 2000) in females. Thus, even in a species with moderate SSD, selective pressures can act very differently on each sex.

7.5 Summary and conclusions

We have shown that estimation of the direction and magnitude of SSD in spiders strongly depends on the size measure chosen, but also that this has probably no large effect in phylogenetic comparative analyses. Whenever possible the use of carapace width is recommended, as this structural measure is common and less affected by condition than body mass or length. Our updated evaluation of body-size allometry supports previous work in demonstrating that spiders do not exhibit allometry consistent with

Rensch's rule. Instead, females appear to have diverged more in size over evolutionary time, and male and female body size show relatively uncorrelated coevolution, which is unusual for animals. This finding requires further research. Quantitative genetic analyses of sex-specific growth strategies are urgently needed if we are to understand the role of genetic constraints in the evolution of extreme SSD. Although much progress has been made over the past 10 years, our knowledge is very patchy with regard to the various hypotheses proposed to affect sex-specific selection. So far, fecundity selection favoring large size in females and gravity selection favoring small size in males are probably the only hypotheses that have some general explanatory power. Nevertheless, many different processes are operating in different species and SSD requires a case-by-case explanation. Importantly, attempts should be made to gain a comprehensive view of selection operating on male and female size in any given species. We hope that this review will stimulate such work.

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7.7 Suggested readings

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