No association between sexual size dimorphism and life histories in spiders

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In spiders, females are commonly larger than males. The majority of hypotheses that attempt to explain sexual size dimorphism in spiders concentrate on reduction in male size, although there is evidence to suggest that the independent evolution of marked sexual size dimorphism and reversion to a less extreme dimorphic state has occurred several times. Recent debate has centred on two conflicting hypotheses involving male dwarfism and increased female size through fecundity selection, and has focused on the golden orb-weaving spider, *Nephila clavipes* (Tetragnathidae), and its relatives. In *Nephila*, males are tiny in comparison to females, however, other orb-web spiders do not show such extremes in dimorphism. Here, we incorporate phylogeny into a comparative investigation of the patterns of sexual dimorphism predicted by the hypothesis of male dwarfism via sex-linked differential mortality during mate searching and note an absence of supporting evidence. There was no evidence of the predicted association between male and female size and sexual size dimorphism with life histories, exemplified by variation in predatory strategies, in spiders.

Keywords: sexual dimorphism, spiders, life histories, phylogeny, independent contrasts

1. INTRODUCTION

Explanations of sexual size dimorphism in spiders, where females are commonly larger than males (Vollrath & Parker 1992; Head 1995; Prenter *et al.* 1997), especially in web spiders, usually concentrate on the reduced size of males in comparison to females (e.g. Darwin 1871; Gerhardt 1924; Levi 1975; Robinson & Robinson 1980; Vollrath 1980; Downes 1981; Jocqué 1983; Main 1990; Elgar *et al.* 1990; Elgar 1991; Vollrath & Parker 1992; Elgar & Fahey 1996). A few studies, however, advocate increased female size (Coddington 1994; Head 1995; Hormiga *et al.* 1995; Prenter *et al.* 1995). Vollrath & Parker (1992) proposed a general model of male dwarfism in spiders. Life history data were used to indicate the evolution of extreme sexual size dimorphism in spiders with sedentary adult females and wandering adult males. Mate-searching males were supposed to experience increased mortality, which biased adult sex ratios towards females. Consequently, male–male competition for mating opportunities is reduced and, thus, selection should favour early maturation in males, leading to dwarfing of male body size. A key prediction of the model is that sit-and-wait predators (web-builders and ambushing crab spiders) should be more dimorphic than active, hunting predators (e.g. wolf spiders).

Recent debate about the evolution of sexual size dimorphism in spiders has centred on the genus *Nephila*, with Vollrath & Parker (1992, 1997) advocating reduction in male size via the mechanism outlined above, whereas

Coddington *et al.* (1997) reject this explanation and favour the idea of increased female size. Although Vollrath & Parker presented evidence of an association between sexual size dimorphism and life histories, they treated species as independent datum points, disregarding the effect of phylogenetic relationships in the data (Coddington *et al.* 1997; Prenter *et al.* 1997) which may serve to artificially inflate sample size and lead to erroneous acceptance of statistical significance (Harvey & Pagel 1991; Brooks & McLennan 1991). Caution against accepting Vollrath and Parker's supporting evidence is advised (Coddington *et al.* 1997) until phylogenetic relationships in the data are properly considered.

Here, we report the results of a comparative analysis of size and sexual size dimorphism in 407 mainly tropical and subtropical spiders from Australasia. We account for phylogenetic relationships by using comparative analysis by independent contrasts (CAIC) (see Harvey & Pagel 1991; Felsenstein 1985; Pagel & Harvey 1989 for details and assumptions) and examine patterns of sexual size dimorphism with respect to foraging or hunting method and life history differences between the sexes.

2. METHODS

A comparative data set comprising measures of body size (length) and sexual size dimorphism (measured as the ratio of female to male size, F/M) for 407 species of spiders from Australasia was compiled from the literature (Singapore; Koh 1996; Australia; Mascord 1970; Japan; Shinkai & Tanaka 1984). Table 1 summarizes the data. Where ranges of size were available in these sources, we used the maximum of the range for males and females. These data included extremely dimorphic

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Table 1. *Summary of data on male and female size (mm) and sexual size dimorphism (F/M) for 37 families of spiders from Australasia with information on foraging mode (For. Mode).*

(S indicates sit-and-wait, H indicates active hunting. Any within family variation (*) is not reflected by the foraging strategy data presented here.)

family	genera	species	female ($\pm$ s.e)	male ($\pm$ s.e)	SSD (F/M) ($\pm$ s.e)	For. Mode
Theridiidae	16	42	6.42 (0.77)	4.45 (0.49)	1.45 (0.05)	S*
Araneidae	23	97	12.04 (0.61)	6.16 (0.35)	2.42 (0.22)	S
Salticidae	34	52	8.23 (0.34)	6.97 (0.29)	1.19 (0.02)	H*
Agelenidae	2	2	13.50 (1.50)	11.00 (1.00)	1.23 (0.03)	S
Lycosidae	10	21	11.52 (0.90)	8.71 (0.62)	1.32 (0.04)	H*
Amaurobiidae	3	4	12.75 (2.29)	8.75 (1.18)	1.44 (0.11)	S
Ctenidae	1	1	11.00 (0.00)	10.00 (0.00)	1.10 (0.00)	H
Anyphaenidae	1	2	7.50 (0.50)	6.50 (0.50)	1.16 (0.02)	H
Segestriidae	2	2	7.50 (0.50)	6.00 (0.00)	1.25 (0.08)	H
Linyphiidae	7	9	4.61 (0.75)	4.12 (0.56)	1.10 (0.06)	S
Thomisidae	20	50	7.16 (0.35)	4.76 (0.25)	1.55 (0.06)	S
Clubionidae	4	13	11.39 (1.30)	8.39 (0.81)	1.35 (0.05)	H
Anapidae	1	1	3.50 (0.00)	2.20 (0.00)	1.59 (0.00)	S
Pholcidae	5	6	6.17 (0.60)	5.00 (0.37)	1.23 (0.08)	S
Sparassidae	8	12	23.92 (2.54)	17.67 (1.75)	1.37 (0.05)	H
Dictynidae	3	3	3.83 (0.60)	3.17 (0.44)	1.21 (0.02)	S
Deinopidae	2	4	15.50 (3.52)	11.00 (2.04)	1.38 (0.09)	S
Pisauridae	5	7	15.14 (2.59)	11.71 (1.49)	1.28 (0.11)	H
Gnaphosidae	6	6	15.17 (2.96)	10.75 (1.80)	1.39 (0.04)	H
Tetragnathidae	11	33	14.06 (1.58)	7.62 (0.54)	1.95 (0.20)	S
Dysderidae	1	1	14.00 (0.00)	11.00 (0.00)	1.27 (0.00)	H
Leptonetidae	1	1	2.50 (0.00)	2.00 (0.00)	1.25 (0.00)	S
Uloboridae	3	7	5.86 (0.42)	4.86 (0.40)	1.22 (0.03)	S
Mimetidae	2	2	7.05 (1.05)	5.10 (0.10)	1.38 (0.18)	H
Mysmenidae	1	1	1.20 (0.00)	1.00 (0.00)	1.20 (0.00)	S
Nesticidae	1	1	2.70 (0.00)	2.00 (0.00)	1.35 (0.00)	S
Oxyopidae	1	5	9.60 (1.17)	7.60 (1.03)	1.29 (0.06)	H
Philodromidae	3	7	8.43 (0.90)	6.86 (0.71)	1.23 (0.03)	H
Liocranidae	1	1	3.50 (0.00)	3.00 (0.00)	1.17 (0.00)	H
Psechridae	1	1	17.00 (0.00)	16.00 (0.00)	1.06 (0.00)	S
Scytodidae	1	3	6.83 (1.26)	4.67 (0.67)	1.52 (0.25)	H
Selenopidae	1	2	11.00 (2.00)	7.50 (0.50)	1.46 (0.17)	H
Zodariidae	1	2	12.50 (3.50)	9.50 (1.50)	1.29 (0.16)	H
Hersiliidae	2	1	8.50 (1.50)	6.00 (2.00)	1.50 (0.25)	H
Oecobiidae	1	1	2.00 (0.00)	1.50 (0.00)	1.33 (0.00)	H
Theridiosomatidae	1	1	2.00 (0.00)	1.50 (0.00)	1.33 (0.00)	S
Zoridae	1	2	5.50 (0.50)	4.00 (0.50)	1.38 (0.05)	H
<i>N</i>	187	407	n/a	n/a	n/a	n/a

species, the vast majority of which may be described as being of tropical or subtropical distribution. Many of the species used here would also have been included in Vollrath & Parker (1992). We used CAIC (Harvey & Pagel 1991; Felsenstein 1985; Pagel & Harvey 1989; Pagel 1992; Purvis & Rambaut 1994) to investigate patterns of sexual size dimorphism with respect to foraging/hunting method and differences between the sexes in life history. This allows statistical comparison by calculating contrasts in the data that are independent of phylogenetic associations (Harvey & Pagel 1991; Brooks & McLennan 1991; Purvis & Rambaut 1994). Information on foraging behaviour was gleaned from the original sources of the data (see above), Nentwig (1987) and the taxonomic glossary of Shear (1986). In the few cases where such information was not available, we assigned individual species to the category of behaviour observed in the genus or family.

Data were logarithmically transformed prior to statistical analysis and, in the absence of evidence to the contrary, we assumed branch lengths in the working phylogeny were equal for the purposes of the CAIC. Estimating branch lengths (e.g. Grafen 1989) in the phylogeny (taxonomy) or assuming they are equal, often does not affect the results (Garland *et al.* 1992). Phylogeny was estimated using available current taxonomy. The general scheme of Coddington & Levi (1991) formed the basis of the taxonomy used, with amendments to the Tetragnathidae according to Hormiga *et al.* (1995). It should be noted, however, that while the latter analysis was based on rigorous cladistic methodology, the former was not so rigorous. Nonetheless, as the basis for a taxonomy for the Araneae, Coddington & Levi's scheme has been successfully used in other studies that are similar to the present one (e.g. Marshall & Gittleman 1994; Head 1995).

Regression analysis on independent contrasts for size and dimorphism were forced through the origin (Harvey & Pagel 1991). Overall size was controlled for in tests of association between sexual size dimorphism in spiders and hunting strategy by regressing independent contrasts for dimorphism and female size. The slope of this regression was fitted to the raw species data, residuals were then calculated and compared with the life history data (Purvis & Rambaut 1994), allowing allometry-free comparisons to be made (Harvey & Pagel 1991; Marshall & Gittleman 1994). Two-tailed Sign tests were used to examine possible association between independent contrast scores for size and dimorphism and variation in life histories. Vollrath & Parker's male dwarfism via differential male mortality hypothesis predicts greater dimorphism in sit-and-wait predators (web-builders and ambushing crab spiders) than in active hunting spiders. Our null hypotheses, therefore, were that female size, male size and sexual size dimorphism, were not linked to the evolution of the life history differences between the sexes, characterized by variation in foraging or hunting strategies.

3. RESULTS

Independent contrasts for female size were significantly and positively associated with both male size ($N=126$, $r^2=0.822$, $F_{1,125}=564.802$, $p<0.00001$; figure 1) and sexual size dimorphism ($N=126$, $r^2=0.159$, $F_{1,125}=23.619$, $p<0.00001$; figure 2). Male size and sexual size dimorphism were not significantly associated ($N=126$, $r^2=0.001$, $F_{1,125}=0.105$, n.s.; figure 3). Crucially, there was no evidence to suggest that any of these three morphological measures differed with variation in foraging strategies. We found no association either between size, of both males and females, and sexual size dimorphism with life histories, exemplified by foraging strategy, in spiders. That is, Sign tests on independent contrasts calculated for male size, female size and sexual size dimorphism did not indicate covariation of size or dimorphism with variation in spider foraging strategy (female size, 7+, 4–; male size, 7+, 4–; sexual size dimorphism, 7+, 4–, all $N=11$, $p>0.5$).

Linear regressions on independent contrasts for size and dimorphism in hunting species ($N=146$) and sit-and-wait spiders ($N=261$) were analysed separately, and showed similar patterns to those for the combined (whole) data set (table 2). In both cases, contrasts for log female size were significantly and positively related to log male size and log sexual dimorphism. A minor difference was evident, however, in the relationship between independent contrasts for log male size and contrasts for log size dimorphism in spiders with different hunting strategies. Contrasts for log male size in hunting spiders was positively, but not significantly, related to contrasts for log size dimorphism (table 2). Although this relationship was also not statistically significant for spiders with a sit-and-wait foraging mode, the relationship was negative (table 2). Comparison of the slopes of the independent contrasts regression for male and female hunting and sit-and-wait spiders by the method outlined in Fowler & Cohen (1996), indicated no significant differences between the slopes of regressions of sexual size dimorphism on female size (figure 4) and male size in hunting and sit-and-wait spiders (figure 5).

Figure 1. Regression of independent contrasts for female size against independent contrasts for male size. The solid line represents the regression equation $y=0.998x$ when the linear regression is forced through the origin.

Figure 2. Regression of independent contrasts for female size against independent contrasts for sexual size dimorphism (F/M). The solid line represents the regression equation $y=0.940x$ when the linear regression is forced through the origin.

Figure 3. Regression of independent contrasts for male size against independent contrasts for sexual size dimorphism (F/M). The solid line represents the regression equation $y=-0.0626x$ when the linear regression is forced through the origin.

Table 2. Summary of linear regressions (forced through the origin) for independent contrasts for female and male size and size dimorphism for spiders with active hunting and sit-and-wait predatory strategies.

(Data were log transformed prior to analysis. * $F_{1,49}$ for hunting spiders and $F_{1,79}$ for sit-and-wait spiders. SSD is sexual size dimorphism.)

	<i>N</i>	r^2	F^*	<i>p</i>	$y =$
hunting spiders					
log female size vs log male size	50	0.914	519.323	<0.0001	0.898x
log female size vs log SSD	50	0.117	6.489	<0.002	0.097x
log male size vs log SSD	50	0.003	0.135	=0.714	0.061x
sit-and-wait spiders					
log female size vs log male size	80	0.758	248.063	<0.0001	0.793x
log female size vs log SSD	80	0.142	16.667	<0.0001	0.206x
log male size vs log SSD	80	0.007	0.543	=0.463	-0.045x

4. DISCUSSION

Coddington *et al.* (1997) provided evidence for the independent evolution of extreme sexual dimorphism and revision to a less extreme state on several different occasions in the orb weavers. They also indicated a shared common ancestry between extant species that currently exhibit extremes of dimorphism. It is important and appropriate, therefore, that we properly accounted for phylogeny, as far as possible, in our examination of dimorphism. Reservations (Coddington *et al.* 1997; Prenter *et al.* 1997) about the validity of the conclusions and assertions made by Vollrath & Parker (1992) based on their species level analysis must, therefore, be repeated. Their supporting evidence would appear to have been confounded by phylogeny (Prenter *et al.* 1997).

Regression using phylogenetically independent contrasts analysis has highlighted and reiterated the positive relationship between female and male size in spiders (figure 1) found in other studies in which phylogeny was accounted for (e.g. Marshall & Gittleman 1994; Head 1995; Prenter *et al.* 1997). Our results, and those of several other studies, also emphasize the importance of female size rather than male size in influencing patterns of sexual size dimorphism in spiders (see Elgar 1991; Coddington 1994; Head 1995; Hormiga *et al.* 1995; Prenter *et al.* 1995, 1997, 1998).

Our data show clearly that sexual size dimorphism is generated by variation in female size (figure 2) and that male size has no significant effect on dimorphism (figure 3). Had sexual size dimorphism been generated by reduced male size, we would have expected the opposite result, i.e. no significant regression between female size and sexual size dimorphism, and a significant negative regression between male size and dimorphism. The most likely explanation of these relationships is that selection for increased fecundity results in increased female size, independent of changes in male size. This latter point is

not entirely predicted. It could be that selection for large female size also results in selection for increased male size (e.g. via increase in egg size commensurate with increased female size), albeit at a lower level, thereby producing the observed pattern of dimorphism. This is subject to the proviso that there is no counter selection for reduced male size. However, the non-significant negative regression between male size and dimorphism explained less than 1% of the variance, and hence this possibility is dismissed.

Head (1995) presented evidence that selection for increased fecundity caused female spiders to be larger than males. Although it would appear that fecundity selection and the advantage of increased fecundity is a general explanation of size dimorphism in spiders (Prenter *et al.* 1998), it is uncertain in how many species patterns of dimorphism are explained by 'female giantism' (Hormiga *et al.* 1995), where females have increased markedly in size to such an extent that males are tiny in comparison.

We found no evidence of the general patterns of dimorphism predicted by Vollrath & Parker (1992, 1997) in our analysis of tropical and subtropical spiders. The differential mortality model does not appear to be capable of explaining patterns of dimorphism present in these spiders or the less extreme sexual size dimorphism that generally occurs in temperate spiders (Prenter *et al.* 1997). The results of comparisons of the regression slopes for male size and dimorphism, and equally for the relationship between female size and dimorphism, between independent contrasts for hunting and sit-and-wait foraging spiders (figures 4 and 5), where no significant differences in slopes were apparent, would also appear to reinforce this conclusion.

The possibility exists that sexual dimorphism, both in extreme (e.g. in the genera *Nephila* and *Argiope*), and less extreme forms (e.g. *Metellina segmentata*; Prenter *et al.* 1995) may have arisen independently under the influence of different mechanisms of selection, for example, through different selective regimes or under phylogenetic constraints. The great variation in male size, which impinges on patterns of sexual dimorphism, could be the result of opposing selection forces for increased (e.g. male-male competition for mates) and decreased male size (e.g. cannibalism reduction; Elgar & Fahey 1996). Alternatively, cases of variation in male size may be the result of different growth and reproductive strategies in males of any species. Further comparative and detailed species-specific investigations, especially of life histories, may help us to elucidate the explanation of the evolution of variation in size and sexual size dimorphism in spiders. Certainly, it is only in such studies that the within-species variation in size, which is generally greater in males (e.g. Faber 1994) can be examined and explained.

It is clear that there has been considerable debate over whether observed patterns of sexual size dimorphism in spiders has arisen through the influence of increased female size (e.g. Vollrath 1980; Head 1995; Hormiga *et al.* 1995; Coddington *et al.* 1997) or reduction in male size (e.g. Main 1990; Vollrath & Parker 1992). Vollrath & Parker (1997) now claim not to have attempted to prove absolute selection for reduced size in males, but rather to predict generally the relative size of the two sexes. There is some

Figure 4. Regressions of independent contrasts for female size against independent contrasts for sexual size dimorphism (F/M) for spiders with active hunting and sit-and-wait predatory modes. The solid line represents the regression equation for data on hunters and the dotted line that for sit-and-wait predators (see table 2 for details).

Figure 5. Regressions of independent contrasts for male size against independent contrasts for sexual size dimorphism (F/M) for spiders with active hunting and sit-and-wait predatory modes. The solid line represents the regression equation for data on hunters and the dotted line that for sit-and-wait predators (see table 2 for details).

limited evidence of dwarf male spiders that mature earlier and that are subject to sex-specific differential mortality (Main 1990; Vollrath & Parker 1997), however, there is still no evidence of the predicted patterns of dimorphism with

respect to life style (foraging mode), and sexual size dimorphism in spiders does not appear to have arisen generally as the result of the process envisaged by Vollrath & Parker (1992, 1997).

It is perhaps now warranted that the process underlying the model, i.e. differential mortality, be the focus of further investigation, rather than the patterns of dimorphism predicted by it. Certainly, such a style of investigation has proved successful in examining variation in male size in *Nephila plumipes*, where Elgar & Fahey (1996) have indicated that the opposing intra- and intersexual forces of selection for increased male size, which are an advantage in male-male contests for mates, and reduced male size which aids the avoidance of sexual cannibalism during courtship, have contrived to produce considerable variation in male size, which itself will be reflected in dimorphism.

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