



Evolution and maintenance of sexual size dimorphism: aligning phylogenetic and experimental evidence

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Integrating the insights derived from both phylogenetic and experimental approaches offers a more complete understanding of evolutionary patterns and processes, yet it is rarely a feature of investigations of the evolutionary significance of trait variation. We combine these approaches to reinterpret the patterns and processes in the evolution of female biased sexual size dimorphism in Nephilidae, a spider lineage characterized by the most extreme sexual size dimorphism among terrestrial animals. We use a molecular phylogeny to reconstruct the size evolution for each sex and reveal a case of “sexually dimorphic gigantism”: both sexes steadily outgrow their ancestral sizes, but the female and male slopes differ, and hence sexual size dimorphism steadily increases. A review of the experimental evidence reveals a predominant net selection for large size in both sexes, consistent with the phylogenetic pattern for females but not for males. Thus, while sexual size dimorphism in spiders most likely originates and is maintained by fecundity selection on females, it is unclear what selection pressures prevent males from becoming as large as females. This integrated approach highlights the dangers of inferring evolutionary significance from experimental studies that isolate the effects of single selection pressures.

Keywords: male-male competition, animal contests, female gigantism, male dwarfism, sexual cannibalism, *Nephila* spiders, Nephilidae

INTRODUCTION

Integrating insights from both phylogenetic and experimental approaches offers a more complete understanding of evolutionary patterns and processes, yet this is rarely a feature of investigations into the evolutionary significance of trait variation (Weber and Agrawal, 2012). The significance of this approach is that it reveals whether micro-evolutionary processes identified through field and laboratory experiments align with the macro-evolutionary patterns suggested by phylogenetic analyses (e.g., Arnqvist and Rowe, 2002). Such an approach requires broadly similar experiments to have been conducted across a range of species, for which there is also a robust phylogeny. Recent developments in systematics, together with the ease of sequencing, have significantly improved our capacity to integrate these approaches (Weber and Agrawal, 2012).

Sexual size dimorphism is particularly well suited to this kind of integrated analysis because measures of the trait are consistent between species and across experimental and comparative studies. The nature and direction of sexual size dimorphism reflects an intricate interplay of natural and sexual selection operating at various hierarchical levels (Darwin, 1871; Arak, 1988; Eberhard, 1996; Blanckenhorn, 2000, 2005; Fricke et al., 2010; Stillwell et al., 2010). Among invertebrates, for example, fecundity selection may favor large female size, while sexual selection

through male-male competition may favor large male armaments that must be supported by larger body size. Natural selection might also act differently on each sex, placing upper or lower limits to body size. The resulting sexual size dimorphism will reflect differences in the strength of these selection components.

The spider family Nephilidae (Figure 1) has among the most extreme examples of sexual dimorphism (Elgar, 1991, 1992; Coddington et al., 1997; Kuntner et al., 2008); for example, female *Nephila pilipes* are on average 125 times heavier than males (Kuntner et al., 2012b). Such extreme female biased sexual size dimorphism has attracted numerous experimental and correlational studies to investigate the role of natural and sexual selection on size evolution in this clade (Kuntner et al., 2013). These studies have identified a number of potential fitness components influencing male and female body size, including fecundity, developmental rates, mate search, male-male competition, sperm competition, and sexual cannibalism (reviews in Elgar, 1992; Elgar and Schneider, 2004; Foellmer and Moya-Larano, 2007; Schneider and Fromhage, 2010; Schneider and Andrade, 2011). An earlier comparative study revealed no phylogenetic correlation between male and female size in nephilid spiders, with a steady evolution toward female gigantism but no clear trend for male size (Kuntner and Coddington, 2009). However, this study had several shortcomings: most notably, it derived from morphological



FIGURE 1 | Female biased sexual size dimorphism in nephilid spiders: From left to right, small males on females in *Herennia etruscilla*, *H. multipuncta*, *Nephila inaurata*, and *N. pilipes*.

and behavioral character data (Kuntner et al., 2008) that lack a temporal perspective and branch length information, crucial for comparative tests (Garland et al., 2005). Further, sexual size dimorphism was one of the characters used for tree searches to create the phylogeny, so analyses of the evolutionary patterns of the trait are not independent of the underlying phylogeny.

We here review the nature and direction of selection pressures identified by experimental studies and compare these patterns against those revealed by contemporary phylogenetic analyses. In particular we use a new molecular, species level phylogeny of nephilid spiders that adds a time perspective and branch length information to a revised topology (Kuntner et al., 2013). Specifically, we test whether male and female size evolution is decoupled and whether the evolutionary trends of male and female size correspond with the selection pressures identified in the experimental studies.

MATERIALS AND METHODS

COMPARATIVE METHODS

We use a recent, molecular nephilid phylogeny, inferred from over 4000 nucleotide characters, which proved robust in sensitivity analyses that also included total evidence (combined molecular and morphological datasets) (Kuntner et al., 2013). We pruned this reference phylogeny for most outgroup taxa, retaining only the “zygiellid” outgroup clade sister to nephilids, and for redundant ingroup taxa. We then updated the datasets on male and female size and sexual size dimorphism for novel evolutionary reconstructions and coevolutionary analyses (Felsenstein, 1985) on this tree.

The size data (Table S1) derive from Kuntner and Coddington (2009), but with additional data for *Phonognatha graeffei* (male mean 5.0 mm, $n = 5$; female mean 7.9 mm, $n = 10$) from Dondale (1966), for *Zygiella x-notata* from Hormiga et al. (2000), for *Clitaetra thisbe* male (2.57 mm, $n = 1$) from Dimitrov et al. (2009), for *Herennia oz* female (11.6–13.6 mm, $n = 2$) from Kuntner (2005), and for *Nephilingis* spp. (Kuntner and Agnarsson, 2011): *N. livida* female 15.5–23.6 mm ($n = 10$), male 3.1–4.9 mm ($n = 10$), *N. borbonica*: female 14.1–21.8 mm ($n = 4$), 3.8–6.1 mm ($n = 2$), *N. dodo*: female total length from 22.6–23.4 mm ($n = 2$), male total length from 4.6–6.6 mm ($n = 3$). Following Kuntner and Coddington (2009), sexual size

dimorphism is expressed as the ratio of female to male average body size.

We explored coevolutionary patterns of continuous variables using phylogenetically independent contrasts (Felsenstein, 1985; Garland et al., 1992) in the PDAP module of Mesquite version 2.75 (Maddison and Maddison, 2012). The size data passed the PDAP test for data conformity, with the exception of male size correlating with its SD using one tailed t -value. We therefore used the inferred, untransformed branch lengths on the Bayesian nephilid baseline phylogeny (Kuntner et al., 2013) in combination with two tailed t -values. Character evolution reconstructions were visualized using squared change parsimony in Mesquite. Values optimized at nodes were assigned to cladogenetic events counting from the phylogenetic root (cladogenetic event = 0) through internal nodes toward the terminal taxa in the phylogeny. The phylogeny postulated a total of 10 cladogenetic events (Figure 2; 0–9). These are taken to roughly represent a temporal scale for the size evolution, corresponding to an evolutionary history of 40–60 million years estimated for the family (Kuntner et al., 2013).

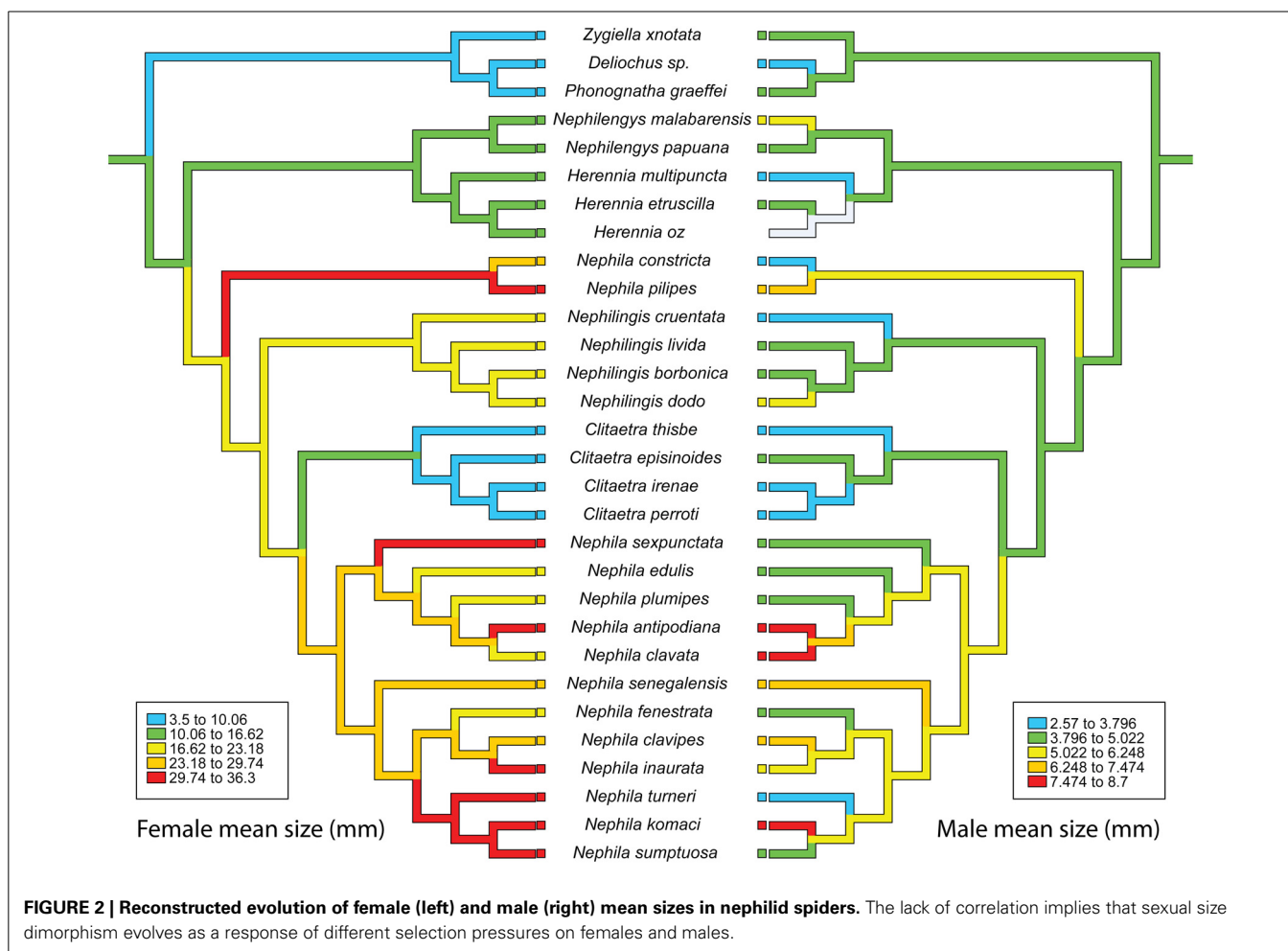
EXPERIMENTAL STUDIES

We searched for original papers investigating the impact of male and female body size variation on female fecundity, and male mate searching, courtship, and mating behavior of any nephilid taxon (*Nephila* and *Nephilingis* species) and relevant outgroups (*Phonognatha*).

RESULTS AND DISCUSSION

COMPARATIVE PATTERNS

Male and female size changes were not phylogenetically correlated [$r^2 = 0.05$, $t = 1.24$, $F_{(1, 27)} = 1.5$, 2-tailed $P = 0.23$; Figure 2]. The lack of correlation implies that sexual size dimorphism in nephilids evolved as a response to selection pressures that differed between the sexes (Hormiga et al., 2000; Kuntner and Coddington, 2009). These results, however, do not reveal the direction of size change in each sex. The reconstruction of evolutionary changes in female and male size from all phylogenetic nodes (leading to all terminal taxa) showed a steady overall increase in female size [$r^2 = 0.155$, $\beta = 1.35$, $F_{(1, 51)} = 9.39$, $P = 0.004$; Figure 3A], and a slight increase in male size over time



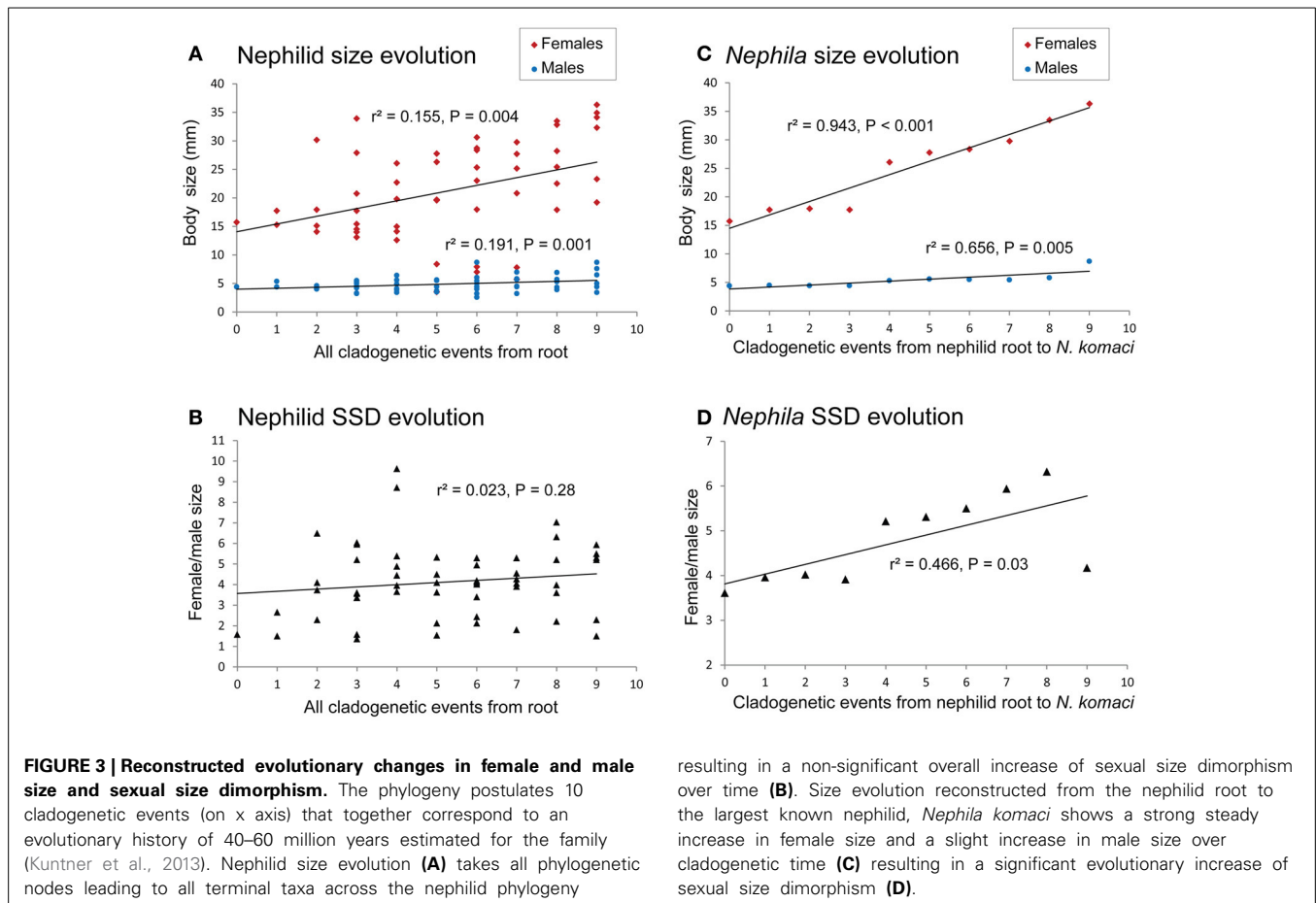
[$r^2 = 0.191$, $\beta = 0.233$, $F_{(1, 41)} = 11.58$, $P = 0.001$; **Figure 3A**]. These slopes are significantly different [ANCOVA: sex by cladogenetic event, $F_{(1, 100)} = 6.09$, $P = 0.015$]. The evolutionary result is a trend toward overall increase of sexual size dimorphism over time (**Figure 3B**). Since parts of the phylogeny may conceivably exhibit different trends in size evolution, we also reconstructed the evolution of female and male size on a selected cladogenetic route leading to extreme female gigantism, that is on a phylogenetic backbone leading from the nephilid root to *Nephila komaci*, the largest known nephilid (Kuntner and Coddington, 2009). This reconstruction showed that over evolutionary time, there was a strong steady increase in female size [$r^2 = 0.943$, $\beta = 2.351$, $F_{(1, 9)} = 133.05$, $P < 0.001$; **Figure 3C**] and a less pronounced increase in male size [$r^2 = 0.656$, $\beta = 0.344$, $F_{(1, 9)} = 15.24$, $P = 0.005$; **Figure 3C**]. Again, these slopes are significantly different [ANCOVA: sex by cladogenetic event, $F_{(1, 16)} = 81.74$, $P < 0.001$]. From the root to the tip of the giant *Nephila* clade, sexual size dimorphism shows a significant evolutionary increase [$r^2 = 0.466$, $\beta = 0.218$, $F_{(1, 9)} = 6.973$, $P = 0.03$; **Figure 3D**].

EXPERIMENTAL EVIDENCE

Experimental and observational studies on *Nephila* suggest that selection should generally favor larger than ancestral size for both

sexes (**Table 1**). However, there is little consistency in these patterns across different *Nephila* species. Contrary to conventional wisdom, evidence for fecundity selection is demonstrated in only three of six species, despite the phylogenetic evidence for strong selection on female size. Intriguingly, the phylogenetic analysis reveals an evolutionary decline in size in the three species (*N. edulis*, *N. plumipes* and *N. fenestrata*) for which there is no evidence of fecundity selection, and either no change (*N. clavipes*, *N. senegalensis*) or an increase (*N. pilipes*) in size in those species for which there is evidence of fecundity selection. It would be worth testing this trend in other nephilids for which we lack any evidence for the strength of fecundity selection. For example, one would predict strong fecundity selection in those species that have made the most contribution to the general increase in female size (**Figure 2**): *N. sexpunctata*, *N. antipodiana*, *N. inaurata*, and the clade with African giants (*N. turneri*, *N. komaci*, *N. sumptuosa*). On the other hand, we predict relaxed fecundity selection in species/clades that show female size decrease (**Figure 2**): *N. clavata*, *N. constricta*, and in *Clitaetra* species.

The evidence for males is even more equivocal: five of six species show a large size advantage in male-male competition, but whether this translates into greater paternity is unclear because



two of four studies reveal an advantage of small size under sperm competition. Further, experimental studies in which both pre- and post-insemination selection pressures can act together over a longer time revealed no comparative advantage for small or large males (Schneider and Elgar, 2005; Elgar and Jones, 2008). Finally, only one of two studies that investigated mate search revealed a large size advantage, and studies of two species indicated that large males were more likely to avoid sexual cannibalism.

SYNTHESIS

The conventional phylogenetic view of the origin of female biased sexual size dimorphism in spiders is through an evolutionary increase in female size, an evolutionary decrease in male size, or both (Coddington et al., 1997; Hormiga et al., 2000). Our phylogenetic analysis reveals an increase in the size of both female and male nephilids. This result, together with the evidence from experimental studies, does not support the view that sexual size dimorphism in this clade is an outcome of male dwarfing (Vollrath, 1998; Danielson-Francois et al., 2012). Rather, it reflects a pattern of sexually decoupled size evolution (Kuntner and Coddington, 2009), not through male evolutionary stasis (Hormiga et al., 2000; Kuntner and Coddington, 2009), but with male and female body size increasing at different rates. This new macro-evolutionary pattern may be described as *sexually dimorphic gigantism*.

The disparity between the macro-evolutionary patterns, revealed by our phylogenetic analysis, and the micro-evolutionary processes identified by experimental studies is instructive. For example, the large size advantage in competitive interactions between males identified in five of six species of *Nephila* is consistent with numerous studies of taxonomically diverse species that are not characterized by extreme sexual size dimorphism (Hardy and Briffa, 2013). But the *Nephila* data simply do not align with either the natural history of this clade (extreme sexual size dimorphism), or the macro-evolutionary patterns (a significantly more modest increase in male size compared with female size). Perhaps these experimental results are evolutionarily trivial because they focus on single components of selection that have little impact on macro-evolutionary processes. Indeed, experiments that combined pre- and post-insemination selection pressures revealed no relationship between male size and paternity share (Schneider and Elgar, 2005; Elgar and Jones, 2008).

Our understanding of sexual size dimorphism has converged on the equilibrium model (Blanckenhorn, 2000), suggesting that a combination of selection pressures is expected to operate on spider males (Foellmer and Moya-Larano, 2007). Combined, they must push male size down, hence the detected genetic decoupling of male and female size evolution in nephilid spiders. If the sizes were genetically linked in both sexes, as is the default in animals (spiders not being an exception, see Uhl et al., 2004), the slopes

Table 1 | Summary outcome of experiments investigating size advantages for each sex of nephilid spiders and selected outgroups.

Taxon	Female fecundity	Mate search	Male-male competition	Sperm competition	Sexual cannibalism	References
<i>N. clavata</i>			Large size advantage in competitive interactions (overall $p < 0.001$) (Miyashita, 1993)			Miyashita, 1993
<i>N. clavipes</i>	Large size: $r^2 = 0.8$, $p < 0.01$, $n = 17$ (Higgins, 1992); $r^2 = 0.2$, $p < 0.01$, $n = 39$ (Rittschof, 2010)	Large males arrived earlier: $F_{(1,29)} = 11.06$, $p = 0.002$ (Ceballos Meraz et al., 2012)	Larger males were at the hub and mated more frequently, $p < 0.01$ (Christenson and Goist, 1979)			Christenson and Goist, 1979; Vollrath, 1980; Higgins, 1992, 2000; Rittschof, 2010; Constant et al., 2011; Ceballos Meraz et al., 2012
<i>N. edulis</i>	No effect: $p = 0.37$; $n = 37$ [19]; $F_{(1, 59)} = 0.5$; $p = 0.5$ (Jones and Elgar, 2008)		Large males excluded small males, $\chi^2 = 24.0$, $p < 0.001$, $n = 30$ (Elgar et al., 2003b)	Small size advantage, $r_s = -0.3$, $p < 0.004$, $n = 86$ (Schneider et al., 2000)	Cannibalized males tend to be smaller: $Z = 1.88$, $p = 0.06$ (Elgar et al., 2003b); $\chi^2 = 6.52$, $p = 0.01$ (Jones and Elgar, 2008)	Schneider et al., 2000; Elgar et al., 2003b; Elgar and Jones, 2008; Jones and Elgar, 2008
<i>N. fenestrata</i>	No effect (Fromhage and Schneider, unpublished data)		Large size advantage: $G = 4.15$, $p < 0.04$; $G = 14.4$, $p < 0.0001$, $n = 22$ (Fromhage and Schneider, 2005)			Fromhage and Schneider, unpublished data; Fromhage and Schneider, 2005
<i>N. inaurata</i>				Small males copulate for longer: $r_s = -0.59$, $n = 23$, $p = 0.003$ (Schneider et al., 2005)		Schneider et al., 2005
<i>N. pilipes</i>	Large size: $r^2 = 0.8$, $p < 0.01$, $n = 6$ (Higgins, 2002)		No effect: Wald = 1.11, $p = 0.29$ (Danielson-Francois et al., 2012)	No effect: $t = 1.31$, $p = 0.2$, $n = 20$, (Danielson-Francois et al., 2012)		Higgins, 2002; Danielson-Francois et al., 2012
<i>N. plumipes</i>	No effect, prosoma: $r^2 = 0.02$, $p > 0.5$, $n = 50$ (Schneider and Elgar, 2002)	No effect, randomization test, $p = 0.19$ (Kasumovic et al., 2007)	Large size advantage: $\chi^2 = 8.22$, $p < 0.001$, $n = 12$ contests (Elgar and Fahey, 1996)		Cannibalized males were larger $t_{(7)} = 3.3$, $p = 0.002$ (Schneider and Elgar, 2001)	Elgar and Fahey, 1996; Schneider and Elgar, 2001, 2002; Elgar et al., 2003a; Kasumovic et al., 2007; Prenter et al., 2010
<i>N. senegalensis</i>	Large size—unpublished (Neumann et al., unpublished data)			No effect		Neumann et al., unpublished data; Schneider and Michalik, 2011; Schneider et al., 2011
<i>Nephilingis livida</i>			No effect			Kralj-Fišer and Kuntner, 2012
<i>P. graeffei</i>	Large size: $F_{(1, 50)} = 5.9$, $p < 0.02$ (Fahey and Elgar, 1997)		Large size advantage: $\chi^2 = 19.2$, $p < 0.001$, $n = 30$			Fahey and Elgar, 1997
Totals for <i>Nephila</i>	Large size: 3/6 (50%)	Large: 1/2 (50%)	Large male: 5/6 (83%)	Small: 2/4 (50%)	Equivocal	

No correlation between male size and total sperm number of virgin males in *N. pilipes* (Danielson-Francois et al., 2012).

would not significantly differ and the independent contrasts test would not show independence, as observed here. The question future studies should be posing, then, is what maintains small male size and thus high sexual size dimorphism? In other words, in spite of the macro-evolutionary trends to increase in size, why are the males not giants, as are the females? Extreme sexual size dimorphism is not typical of species of orb-weaving spiders with large females: there is modest sexual size dimorphism in the orb-weaver genus *Eriophora*, in which adult females are of similar size to *Nephila* (Elgar, 1991). Thus, future experimental studies might profitably focus on selection pressures that could disfavor large male body size, including those that may arise through conflict with female interests, dispersal between webs and long-term survival.

Several authors have suggested that small male size is favored in response to sexual cannibalism (Elgar, 1991), protandry (Danielson-Francois et al., 2012; Elwood and Prenter, 2013), or gravity (Moya-Larano et al., 2002, 2009; Corcobado et al., 2010), but these ideas have attracted either little attention or no empirical support (Table 1; see also Prenter et al., 2010). Perhaps the low variance in male mating success that frequently characterizes the mating system of these spiders limits the opportunity for selection on male size. In many nephilid species, male genitalia are damaged during mating, leaving the male incapable of further mating and his broken remnants acting as a total or partial mating plug (Kuntner et al., 2009, 2012a). The exceptions may provide insights: both males and females of *N. edulis* mate multiply, and single interaction experimental studies reveal both large (Elgar et al., 2003b) and small (Schneider et al., 2000) male size advantages that are counter-balanced over the longer term (Schneider and Elgar, 2005; Elgar and Jones, 2008). Sexual dimorphism is extremely variable in this species, with some males roughly an order of magnitude larger than other males (Elgar et al., 2003b). Perhaps multiple mating by both sexes in this species provides a greater opportunity for selection to act on male size variation. Intriguingly, *N. senegalensis*, *N. inaurata* and *N. clavipes* have similar variation in male size (Higgins et al., 2011), and it would be interesting to investigate the impact of male size on male mating success over the longer term (following Elgar and Jones, 2008) in these species.

OUTLOOK

Our study highlights the benefits of integrating insights derived from phylogenetic, comparative and experimental research. Like many studies of phenotypic traits, investigations into the evolutionary significance of sexual size dimorphism in spiders have utilized two methodological approaches, one phylogenetic, the other experimental, with each progressing largely independently. In isolation, phylogenetic and comparative analyses only reveal macro-evolutionary patterns of phenotypic evolution, while experimental studies only highlight population level processes responsible for trait maintenance. Such an insight is not new (Coddington, 1988, 1990), but our capacity to align these approaches is only recently becoming possible (Weber and Agrawal, 2012). For fully integrative studies, experimental and comparative agendas need to define common goals and priorities. Our survey showed that for investigations of sexual size

dimorphism in orb-web spiders, comparative data remain insufficient; experimental work suffers from a lack of selection differentials; and we need far greater taxonomic coverage than selective studies on a handful of model species (see also Zuk et al., 2014).

Despite these shortcomings, the present study shows how a more complex picture of sexual size dimorphism emerges when phylogenetic and experimental evidence are integrated. Selection favors large size in both males and females, but fecundity selection is stronger than the net selection for large male size (Blanckenhorn, 2000; Stillwell et al., 2010). At the scale of 40–60 million years of evolution (Kuntner et al., 2013), the size increases—genetically uncoupled between the sexes—result in a peculiar case of *sexually dimorphic gigantism*. New phylogenetic and experimental evidence will likely provide useful insights, but integrating these approaches is crucial.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <http://www.frontiersin.org/journal/10.3389/fevo.2014.00026/abstract>

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