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Mass-mediated sex differences in climbing patterns support the gravity hypothesis of sexual size dimorphism

J. Moya-Laraño, D. Vinković, C. M. Allard and M. W. Foellmer

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The gravity hypothesis of sexual size dimorphism can explain the patterns of extreme sexual size dimorphism in spiders (males smaller than females) because small males climb faster and therefore may be better at reaching females that live in high habitats. Recently, the main prediction of a negative relationship between climbing speed and body size in spiders has been called into question. Here we induced males and females of the spider *Leucauge venusta* (Tetragnathidae) to run on vertical surfaces and found partial support for the gravity hypothesis. As predicted, males climb faster than females and we demonstrated that this effect is an indirect effect mediated by the negative relationship between body mass and climbing speed. We validate our results using simulated data showing that there is enough statistical efficiency in our data set to support our conclusions. We distinguished between direct and indirect effects (through mass) on sex differences in climbing speed by means of path analysis. Thus, we provide empirical evidence that by being smaller, males are able to climb faster than females. However, we found only a barely significant negative relationship between climbing speed and body size when only males were considered. Reasons for such results are discussed within the text.

J. Moya-Laraño (jordi@eeza.csic.es), Depto de Ecología Funcional y Evolutiva, Estación Exp. de Zonas Áridas, Consejo Superior de Investigaciones Científicas, General Segura, 1, - Almería, ES–04001, Spain. – D. Vinković, Physics Dept, Univ. of Split, N. Tesle 12, Split, CR–21000 Croatia. – C. M. Allard, Dept of Biological Sciences, Clemson Univ., Clemson, SC 29634-0314, USA. – M. W. Foellmer, Dept of Biology, Adelphi Univ., Garden City, NY 11530, USA.

Sexual size dimorphism (SSD), defined as a difference in mean body size of males and females within species, is very common in animals (Abouheif and Fairbairn 1997, Fairbairn 1997). Females are larger than males in most species, but males are typically the larger sex in mammals and birds, and exceptions to these general trends exist (Fairbairn 1997, Fairbairn et al. 2007). One of the great enigmas has been the extraordinary range and degree of SSD found in spiders (Vollrath and Parker 1992, Coddington et al. 1997, Foellmer and Fairbairn 2005a, Foellmer and Moya-Laraño 2007). The spiders (Araneae) is the terrestrial animal taxon with the broadest range of SSD and is the only one where extreme SSD is common, with females weighing several hundred times as much as males in a number of genera (Ghiselin 1974, Head 1995, Foellmer and Moya-Laraño 2007). Furthermore, extreme female-biased SSD has evolved several times independently in spiders (Coddington et al. 1997, Hormiga et al. 2000).

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Ultimate explanations of SSD focus on identifying sex-specific patterns of selection, which, if they favor different optimal body sizes in males and females, should lead to the evolution of SSD assuming an imperfect genetic correlation for size between the sexes (Lande 1980, Blanckenhorn 2000, Preziosi and Fairbairn 2000, Reeve and Fairbairn 2001). Body size is one of the most important quantitative traits of an organism because it is strongly correlated with many physiological and life-history traits (Andersson 1994, Blanckenhorn 2005, Blanckenhorn et al. 2007, Teuschl et al. 2007). Due to the different reproductive roles of males and females, optimal body sizes differ for the sexes in most species (Fairbairn 1997, Fairbairn et al. 2007).

Several hypotheses have been put forward to explain the evolution of SSD in spiders (Darwin 1871, Gerhardt 1924, Vollrath and Parker 1992, Coddington et al. 1997, Moya-Laraño et al. 2002). Comparative analyses have lent good support for the fecundity advantage hypothesis, which states that large size in females is favored because of the associated higher reproductive potential (Head 1995, Prenter et al. 1998, 1999). However, it is far from clear what factors have been and/or are responsible for the evolution and maintenance of small male size (relative to female size) (reviewed by Foellmer and Moya-Laraño 2007). This is perhaps not surprising because clear demonstrations of advantages of small body sizes generally are rare in animals (reviewed by Blanckenhorn 2000, 2005; for recent examples see Dibattista et al. 2007, Moya-Laraño et al. 2007). One hypothesis that may hold general explanatory power for the evolution and maintenance of SSD in spiders, and extreme SSD in particular (Foellmer and Moya-Laraño 2007), is the recently proposed gravity hypothesis (Moya-Laraño et al. 2002).

The gravity hypothesis is based on a simple biomechanical model and states that size (mass) is inversely proportional to achievable running speed on vertical structures (Moya-Laraño et al. 2002). Therefore, it predicts that small size should be favored in males during mate search in species where males have to move through a three-dimensional habitat and have to climb to reach females, which is the case in many spider species (Moya-Laraño et al. 2002). The speed advantage of small males should mean that they are better at escaping predators and/or that they reach females faster than larger males and therefore gain an advantage in scramble competition (Moya-Laraño et al. 2002, Ramos et al. 2004). A second prediction of the gravity hypothesis is that female-biased SSD should be more pronounced in species where females build their webs high up in the vegetation than in species where females place their webs close to the ground (Moya-Laraño et al. 2002).

A comparative analysis has supported the prediction of the gravity hypothesis that female-biased SSD should increase with habitat height due to male size effects alone (Moya-Laraño et al. 2002). However, the few studies that have evaluated the effect of male size on a male's ability to locate females directly in field studies have produced mixed results: Small male size was favored (*Nephila clavipes*, Linn 2001), intermediate sized males were most successful (*N. clavipes*, Vollrath 1980), large males were favored by virtue of their relatively longer legs (in one of two populations in *Argiope aurantia*, Foellmer and Fairbairn 2005b), or no significant size effect was detected (*Latrodectus hasselti*, Andrade 2003; *N. plumipes*, Kasumovic et al. 2007). A recent test of the main prediction that larger males would climb at a slower speed than smaller males failed to find any correlation between climbing speed and male body size in *Latrodectus hesperus* (Brandt and Andrade 2007). Therefore, it appears that in most spiders studied to date, male morphology (i.e. size) is unimportant for successfully finding mates, which is difficult to believe (Blanckenhorn 2000, 2005). However, one potential pitfall of using individuals encompassing naturally occurring trait variation in studies is low statistical power, because in the presence of strong selection in the wild, trait values that are selected against can be expected to be rare (Kingsolver 1999, Teuschl et al. 2007).

In this paper we test the main prediction of the gravity hypothesis (i.e. that larger spiders climb at a slower speed) by comparing the climbing speed of males and females of *Leucauge venusta*, a species with intermediate female-biased SSD. By including males and females in the relationship we were able to expand the body mass range from 5–28 mg as used by Brandt and Andrade (2007) to 8–87 mg. This is important and analogous to experimentally increase the range of a trait to increase the power of the test (Kingsolver 1999, Teuschl et al. 2007), particularly if potential differences in motivation, physiology and morphology between the sexes can be ruled out (Discussion). *Leucauge venusta* shows less pronounced SSD than *L. hesperus*, however, because it lives in high bushy vegetation it is an appropriate system for testing the gravity hypothesis. Although we acknowledge that the different reproductive roles of males and females can involve a sex-specific contribution of gravity on the evolution of body size, it is important to stress that the prediction of a negative relationship between body size and speed has to work on any spider, not just on males. A biomechanical model follows universal rules. Thus, it is equally valid to test this prediction focusing on males, females, or even juveniles, as long as sex or developmental stage is statistically controlled for. A different matter is how sex role differences (e.g. higher male need for mobility) will drive SSD, which is not what we are testing here. We hypothesized that a) there should be a negative relationship between climbing speed and body mass within each sex, b) males would climb faster than females, and c) if both sex and body mass were included in the same statistical model explaining climbing speed (e.g. path analysis), the negative relationship between body mass and climbing speed should be significant while the effect of sex should be less important or even disappear.

This later pattern would indicate that males climb faster than females due to the effect of their lighter bodies, as predicted by the gravity hypothesis. In addition, if the effect of sex in this model is close to zero while the effect of mass explains most of the variance of climbing speed, it would mean that differences in muscle building and body shape or differences in motivation would probably not be responsible for the observed pattern.

Material and methods

During June 2002 we ran climbing trials using adult males (n = 10) and females (n = 27) of the tetragnathid *Leucauge venusta*. Females of this species build their webs in forests across North America (Levi 1981) at heights that vary between 50 and 150 cm (Hénaut et al. 2006). Spiders were collected in a mixed deciduous forest in Madison Co., Kentucky, USA. Males of this species are 3.5–4 mm long, whereas females are 5–7.5 mm long (Kaston 1981). Each individual spider was induced to run on a vertical rod (1.20 m high, 3 cm diameter) by carefully placing it on top of the rod (on the 3-cm diameter surface) and gently pushing it down, after which the spider dropped on a silk strand and started climbing sometime after it reached the pole. We carefully cut the silk strand with scissors in order to be sure that, during climbing, the only attaching points were on the rod itself. For each trial, we measured the starting and ending points of a continuous spider race up the pole (> 10 cm) and used a stopwatch for timing. One of us handled the spider while the other handled the stopwatch, thus ensuring enough accuracy in our measurements. After trials, all spiders were weighed to the nearest 0.1 mg, then sacrificed in the freezer and immediately transferred to 70% ETOH. Carapace width (widest part) and body length were measured to the nearest 0.1 mm using an ocular micrometer under a dissection microscope. Instead of measuring body length directly, we measured carapace and abdomen length and summed them up. Because the abdomen of spiders can grow on top of the carapace, our procedure of measuring length likely overestimates length relative to the usual direct measurement. However, we believe that this measurement of length is more accurate because it removes the effect of the angle between the carapace and the abdomen, which can freely rotate around the junction point. Table 1 shows the pattern of SSD as measured from the individuals in our sample. Our animals seemed substantially longer and heavier than those reported by others (Kaston 1981, Hénaut et al. 2006). In any case, SSD is moderately pronounced, and not nearly as strong as in the tetragnathid genus *Nephila*, in which females can be up to four times longer than males (Higgins 2002). However, the range of body sizes (including both males and females) may be large enough to pick up the negative relationship between body mass and speed predicted by the gravity hypothesis.

Table 1. Body size traits (mean ± SE) for the individuals of *Leucauge venusta*. Letters indicate significant differences between the means ($p < 0.0001$).

Trait	Males (n = 10)	Females (n = 27)
Mass (mg)	11.2 ± 0.4^{a}	52.3 ± 3.7^{b}
Carapace width (mm)	1.61 ± 0.02^{a}	1.99 ± 0.03^{b}
Body length (mm)	5.9 ± 0.2^{a}	10.4 ± 0.2^{b}

We tested for a negative relationship between climbing speed and body mass separately for males and females by means of linear regression analysis. The gravity hypothesis makes a main prediction based on body length; however, gravity affects length by virtue on its effect on mass (Foellmer and Moya-Laraño 2007). In other words, length is affected because mostly mass, with which length is highly correlated, is affected. Thus, the hypothesis can be equally tested using mass or body length. Because not all spiders raced for the same length and this could certainly affect their performance, we also considered the potential effect of race length on running speed. The length of the climbing race did not negatively affect the measured speed (both sexes $p > 0.18$). We compared the climbing speed of males and females by means of GLM and type-III sums of squares. As a first approach to distinguish whether sex or mass were more likely responsible for the pattern (prediction c) we included both variables in the model. Sex and body mass were slightly colinear (tolerance ~ 0.4). As colinearity can both substantially decrease power (Graham 2003) and induce bias in parameter estimation (Legendre and Legendre 1998), we ran a simulation to test for type-I and type-II statistical errors in a model with a similar degree of correlation between the variables, same sample sizes and similar effect sizes as estimated here. Simulation procedures followed a very similar approach to that of Moya-Laraño and Wise (2007a) to test the statistical efficiency of inverse logistic regression in ecological experiments.

In short, we ran 100 GLM tests on simulated data of the model Speed = $-0.58 \times \text{mass} + 0 \times \text{sex} + \varepsilon$, where ε is the error in the regression model (standardized normal distribution) with mass and sex showing a degree of tolerance of 0.36. We predicted that for our GLM analysis to be valid, our simulations would have to show sex effects in approximately 5% of the tests (acceptable type-I error rate of 0.05) and mass effects in >>5% of the tests, the exact percentage being and estimate of the statistical power rate. To put in simpler words, this would mean that if mass is the only predictor of speed and sex differences are mediated merely by mass, our GLM would be a statistically efficient test, thus leading to correct conclusions. Similarly, if our simulations were correct, we would have to see relatively high power to detect a sex or a mass effect when these are tested alone, which would indicate that our simulations successfully mimicked an indirect effect of mass on sex differences in running speed. To test for the type-I error rates of mass; that is, to test the proportion of times that mass would show significant in a GLM coming from a population in which mass had no true effect, we also ran 100 GLM test of the model Speed = 0 × mass + 0 × sex + ε, in which again mass and sex had a degree of tolerance of 0.36. Thus, if we show low type-I error rates (< 0.05) for both sex and mass, and some power to detect a true effect of mass, we can conclude that despite sex and mass being correlated, we can reach correct conclusions with our approach. An inspection of our simulated data showed that we obtained similar relative sex differences between mass and climbing speed to those observed in our data set. Even though the distribution of mass and speed was disjoint, both in our data and in our simulations, the error distribution of the residuals was normal, which made the data suitable to GLM. Our hypotheses under test are one tailed (i.e. the alternative hypotheses are males climbing faster than females and a negative relationship between body mass and climbing speed), hence, after validating our approach via simulations based on two-tailed tests, we increased our power even further by performing one-tailed tests.

After validating that we had enough statistical efficiency to work with our data set, we used path analysis including sex as an exogenous variable (male – 1, female – 2) to refine the test of prediction (c) in the Introduction. For path analysis we used the program AMOS 5.0 (Arbuckle and Wothke 1999, Arbuckle 2003). To determine whether the effect of sex on climbing speed was more likely direct (i.e. not through sex mass differences) or indirect (i.e. mostly due to mass differences and thus supporting the gravity hypothesis), we used the principle of parsimony, comparing Akaike's information criterion corrected for small sample size (AICc) between models that had either the direct or the indirect path (Moya-Laraño and Wise 2007b). The model with the lowest AICc is the most parsimonious (Burnham and Anderson 2002).

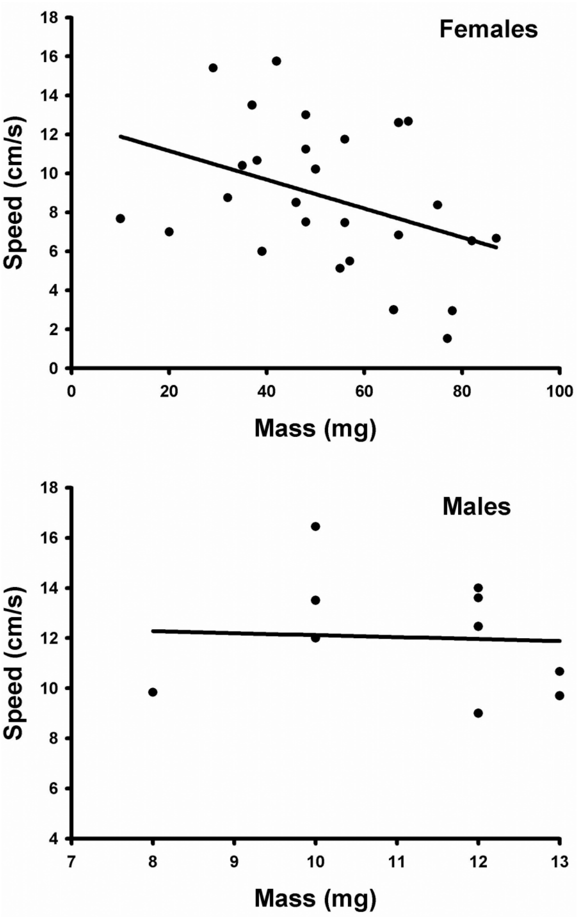

Fig. 1. Linear regressions between body mass and climbing speed in females (top) and males (bottom) of the spider *Leucauge venusta*. The negative relationship for females is significant ($p < 0.05$; Speed = 12.7 – 0.07 × mass). The value for males comes close to signification if the outlier on the far left is removed (see text for statistical analysis).

Results

When considering males and females separately we found a negative relationship between climbing speed and body mass in females ($r = -0.39$, $p = 0.023$, Fig. 1) but not in males ($r = -0.09$, $p = 0.398$). However, after removing an outlier on the far left (Cook's distance = 1.95), the p-value for a negative relationship for males decreased substantially and was barely significant ($r = -0.53$, $p = 0.075$). Also, we found that males climbed 1.4 times faster than females (GLM: $F_{1,35} = 7.1$, $p = 0.006$, Fig. 2). A GLM model including both mass and sex was significant ($F_{2,35} = 6.6$, $p = 0.004$) with a significant negative effect of mass (Beta = –0.50, $F_{1,34} = 5.2$, $p = 0.015$) and a far from significant effect of sex (Beta = 0.04, $F_{1,34} = 0.03$, $p = 0.435$). A model including the interaction (sex × mass) term did not improve the fit, as the interaction was not significant ($F_{1,33} = 0.01$, $p = 0.458$). The GLM simulations showed that the type-I error rate for a sex effect, in a model including both mass and sex, was 0.07 (very close to the desired 0.05), whereas the power to detect a mass effect in a model including mass and sex was 0.41. As expected, when effects were included alone in two separate GLMs, both sex and mass were significant in many of the tests (60 and 81%, respectively), indicating that we successfully simulated an indirect effect of sex on climbing speed mediated by the correlation of sex with mass. In addition, the type-I error rate of mass (in tests coming from a population with no true effect of mass) was 0.03, very close to the desired 0.05. Thus, although we had not very high power to detect the effect of mass (41%), we can be confident that a significant effect is real, and most importantly, that if sex has no direct effect in the model, it will be very unlikely that it shows significant (low type-I error). Finally, path analysis suggested that males climbed faster than females because males are smaller (Fig. 3). A model including the direct path of sex

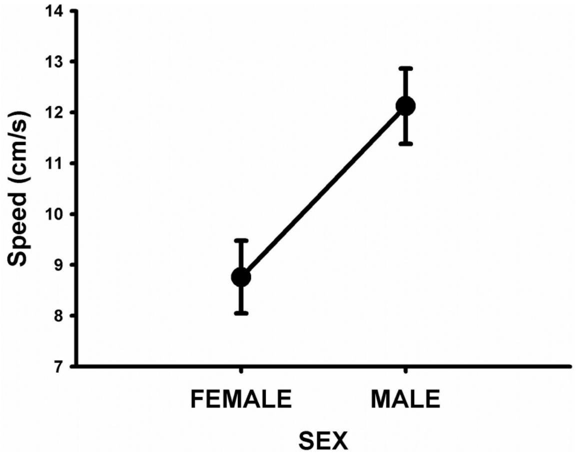

Fig. 2. Differences in climbing speed between males (n = 10) and females (n = 27) of *Leucauge venusta*.

leading to differences in climbing speed is much less parsimonious (AICc = 26.6) than a model including the indirect path of sex leading to differences in mass which lead to differences in climbing speed (AICc = 23.1). In addition, the path connecting mass with climbing speed is negative and significant, supporting the gravity hypothesis.

Discussion

The climbing patterns of male and female *Leucauge venusta* provide partial support for the gravity hypothesis (Moya-Laraño et al. 2002). Although we failed to demonstrate a significant negative relationship between climbing speed and body size in males alone, using an expanded range of body sizes by testing the relationship in females, we found the predicted negative relationship between climbing speed and body size. Importantly, we found that males were 1.4 times faster than females but that this difference was an indirect effect mediated by sex differences in body mass. Our simulations showed that a GLM model had some power to disentangle these two effects and, most importantly, that in spite of mass and sex being tightly correlated, no misleading results (e.g. by committing excessively high type-I errors) could be at play. Thus, our findings indicate that differences in climbing abilities between males and females are mostly due to their differences in body mass, exactly as it would be predicted by the gravity hypothesis. In addition, the fact that sex differences are far from significant once mass is controlled for also demonstrates that sex differences in motivation, physiology or morphology were probably not responsible for the observed pattern because they had an undetectable effect.

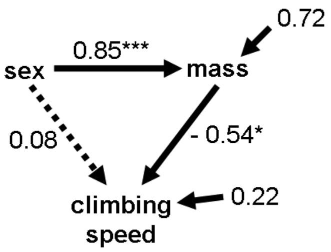

Fig. 3. Path analysis showing the direct and indirect relationship of spider sex with climbing speed. Numbers beside arrows that originate from variables indicate path coefficients. Numbers beside arrows that point to variables, but are not originated from other variables, indicate error (unexplained) variances. The dotted arrow show the least parsimonious direct model (AICc = 26.6) and the continuous arrows the most parsimonious indirect model (AICc = 23.1), supporting the hypothesis that males climb faster than females because males are lighter. *, p = 0.05; ***, p < 0.0001.

The reason why the negative relationship between body size and speed does not arise when using males only (Brandt and Andrade 2007, current study) is intriguing. However, our barely significant result after removing an outlier suggests that the relationship between body size and speed in males would arise with a larger sample size. The gravity hypothesis explains that the strong pattern of SSD found in spiders that live in tall places originated by selection acting against large male body size because smaller males would have a climbing advantage. There are several potential explanations for the lack of a pattern that will have to be investigated in the future. First, the relationship between body size and climbing speed for spiders is not merely a negative one, but when the range of body sizes is expanded beyond that used in this paper, a parabolic relationship between climbing speed and body size arises (Foellmer and Moya-Laraño 2007, J. Moya-Laraño et al. unpubl.). These findings do not contradict the gravity hypothesis, but suggest that it does not apply to very small animals, for which other constraints may be at work. The physiology of climbing, particularly for small animals, is not well understood. We are presently working on a model explaining this curvilinear pattern. It is possible that the animals used by Brandt and Andrade (2007) are near the optimal body size for climbing (i.e. small size range) and that only a large sample size and a curvilinear model will reveal the effect. Obviously, this fact applies also to our own study. In addition, a lack of motivation to climb could be the cause for a high error in our speed measures. Indeed, Brandt and Andrade (2007) found that repeatability in climbing speed was very low in one data set. It is also possible that the pronounced SSD of some spiders was fixed some time during their evolutionary history (when it was adaptive according to the gravity hypothesis) and that, after the breaking of the between-sex genetic correlation for body size, most of the genetic variation for male body size has been eroded. Thus, fitness surfaces would be rather flat; i.e. the ghost of evolution past. Although selection against large body size may still be occurring at present, the effect may be so small and fluctuating that it remains largely undetected with the sample sizes that are logistically achievable in these types of experiments. Brandt and Andrade (2007) provided an alternative model, an explanation to the gravity hypothesis. We argue against the validity of these alternatives somewhere else (Moya-Laraño et al. in press). However, the arguments are too long and beyond the scope of this paper to be discussed here.

In conclusion, our climbing trials with *L. venusta* provided support for the gravity hypothesis that males are smaller than females because this allows males to climb faster: overall there was a negative relationship between climbing speed and body mass, and males climbed faster than females, likely an indirect effect mediated by sex differences in mass.

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