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Optimal climbing speed explains the evolution of extreme sexual size dimorphism in spiders

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Abstract

Several hypotheses have been put forward to explain the evolution of extreme sexual size dimorphism (SSD). Among them, the gravity hypothesis (GH) explains that extreme SSD has evolved in spiders because smaller males have a mating or survival advantage by climbing faster. However, few studies have supported this hypothesis thus far. Using a wide span of spider body sizes, we show that there is an optimal body size (7.4 mm) for climbing and that extreme SSD evolves only in spiders that: (1) live in high-habitat patches and (2) in which females are larger than the optimal size. We report that the evidence for the GH across studies depends on whether the body size of individuals expands beyond the optimal climbing size. We also present an *ad hoc* biomechanical model that shows how the higher stride frequency of small animals predicts an optimal body size for climbing.

Introduction

Understanding the evolution of different phenotypes in conspecific males and females (sexual dimorphism) is of central interest to evolutionary biologists (Fairbairn *et al.*, 2007). Generally, sexual dimorphisms are hypothesized to be the result of the evolution of the sexes in animals and plants, and the consequential divergence of reproductive roles and sex-specific patterns of selection (Andersson, 1994; Fairbairn *et al.*, 2007). Much remains to be explained, however, for example the simple observation that some species show little or no dimorphism, whereas closely related species may show pronounced dimorphism in size, weaponry, or ornamentation (e.g. Andersson, 1994; Delph, 2005; Foellmer & Moya-Laraño, 2007; Kupfer, 2007). One particular evolutionary riddle has been the repeated evolution of extreme sexual size dimorphism (SSD) and the enormous variability and range of SSD in spiders (Araneae) (Head, 1995; Vollrath, 1998; Hormiga *et al.*, 2000; Foellmer & Moya-Laraño, 2007). In most spider species, females are larger than males, as is typical for invertebrates (Fairbairn, 1997; Foellmer & Moya-Laraño, 2007), but SSD ranges from male biased to extreme female biased, with females weighing more than 100 times as much as males – a degree of SSD that is otherwise only seen in marine organisms (Ghiselin, 1974; Vollrath, 1998). Hypotheses trying to provide a general explanation for the adaptive significance (i.e. convergent evolution) of extreme female-biased SSD have been controversial to this date (reviewed in Foellmer & Moya-Laraño, 2007).

The fecundity advantage hypothesis which states that large females benefit from high fecundity is well supported in spiders (Head, 1995; Prenter *et al.*, 1999), and probably as a result of a fecundity advantage females in several spider lineages have increased in size over evolutionary time (Hormiga *et al.*, 2000). Nevertheless, the fecundity advantage hypothesis cannot explain why males have not increased in size along with females as would be expected in the absence of counteracting selection on males, because males and females share

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largely the same genome, i.e. the same genetic basis for growth and development (Lande, 1980; Rhen, 2007). Several hypotheses have been put forward to explain a small-male advantage in spiders (Foellmer & Moya-Laraño, 2007). The sexual cannibalism hypothesis posits that small males have an advantage because they are better able to escape an attacking cannibalistic female or they are not attacked in the first place because they are too small to be detected or to be considered as prey (e.g. Elgar & Fahey, 1996). The differential mortality hypothesis states that males experience a high probability of mortality during mate search which relaxes male–male competition over access to females which selects for large male size in many species (Andersson, 1994). In turn, early maturation at a small size would be favoured in males to increase the probability to reach adulthood (Vollrath & Parker, 1992). Conceptually related to the later hypothesis, Ghiselin's (1974) small male hypothesis posits that male–male competition is relaxed because of the low probability that more than one male reaches a female due to low population densities, and hence early maturation at a small size would be favoured (Ghiselin, 1974). However, none of these hypotheses appears to be able to provide a general explanation as to why extreme SSD has evolved repeatedly (reviewed in Foellmer & Moya-Laraño, 2007), which has led some researches to believe that each case may well require a separate explanation (Hormiga *et al.*, 2000).

It is almost certain that specific patterns of selection will vary from species to species, and hence species-specific optimal body sizes (and therefore SSD) are at least to some degree the result of unique selection pressures. Nevertheless, the repeated independent evolution of an unusual feature such as extreme size differences between males and females suggests that some common form of selection might be the driving factor. Moya-Laraño *et al.* (2002) proposed the gravity hypothesis (GH) for the evolution of extreme SSD in spiders, which states that climbing speed is inversely proportional to body size. Males are the searching sex in almost all spider species and consequently move a lot more than females, especially in web-building spiders (Foelix, 1996; Aisenberg *et al.*, 2007). In species where females live relatively high up in the vegetation, males probably have to run or walk repeatedly on vertical structures such as stems on their voyage through the three-dimensional vegetation structure to find receptive females, irrespective of their original starting point (i.e. below or even above a female that they might eventually find). This is in contrast to males of ground-dwelling species, for example. Therefore, small males are predicted to have an advantage in high-habitat species because they find females faster and/or escape predators better (Moya-Laraño *et al.*, 2002). A second prediction of the GH is that with increasing habitat height, the degree of female-biased SSD should increase. This second prediction was supported by a phylogenetic comparative analysis (Moya-Laraño *et al.*, 2002). However, studies testing directly whether small males are faster climbers than large ones or have an advantage in scramble competition over access to females (i.e. find females first) have yielded mixed results: small males were favoured (Linn, 2001), no size effects were detected (Andrade, 2003; Foellmer & Fairbairn, 2005; Brandt & Andrade, 2007a; Kasumovic *et al.*, 2007), intermediate-sized males were favoured (Vollrath, 1980) and even large males had an advantage (Foellmer & Fairbairn, 2005). Brandt & Andrade (2007a) questioned the validity of the model underlying the GH; however, the alternative model they presented has since been shown to be flawed and unable to describe biological processes (Brandt & Andrade, 2007b; Moya-Laraño *et al.*, 2007a).

Moya-Laraño *et al.* (2007b) tested for a difference in climbing speed between male and female *Leucauge venusta* to overcome the inherent limitation of studies that include only naturally occurring size variation among males, namely that phenotypes at the ends of the size distribution may be rare and rapidly eliminated from the population by selection. This was termed by Blanckenhorn (2005) as the 'ghost of the evolution past', to refer to the fact that the evolutionary processes that we can measure in current time do not necessarily reflect adaptive evolution occurring in the past. Hence, selection against these phenotypes may be very difficult to detect if the range of phenotypic variation is not enhanced experimentally (Kingsolver, 1999; Teuschl *et al.*, 2007). After controlling for confounding effects of sex, Moya-Laraño *et al.* (2007b) found that the small males climb faster than females due to the mass effect alone, as predicted by the GH. Similarly, Foellmer & Moya-Laraño (2007) cited preliminary results of a study testing for the relationship between body size and climbing speed using individuals from various species and developmental stages to maximize the size range of experimental individuals. Surprisingly, they found a curvilinear pattern: climbing speed increased with size in small species until an optimal size value, above which it decreased with size.

Here, we first present the complete analysis of the data set cited in Foellmer & Moya-Laraño (2007). We examine in a phylogenetically controlled comparative analysis whether the experimentally determined optimal body size for climbing speed is reflected in the body size relationship between males and females of spider species, i.e. whether males in tall-habitat species do not evolve beyond this size optimum and thus as a consequence pronounced SSD evolves. We discuss these new findings in the light of the evidence found so far for the GH. Finally, we derive a refined biomechanical model for the relationship between climbing speed and body size that explains the empirically determined curvilinear climbing speed – body size function, as the original GH could not account for this.

Materials and methods

Climbing trials

We collected a sample of spiders belonging to five different families (Tetragnathidae, $n = 18$; Araneidae, $n = 25$; Thomisidae, $n = 4$; Theridiidae, $n = 13$ and Pholcidae, $n = 5$) in houses, old fields and forests around Lexington (KY, USA). As we wanted to maximize the body size range as much as possible within the Araneomorphae (modern) spiders, we used individuals of various instars (as in Moya-Laraño *et al.*, 2008). The mass range of our sample was 0.2–881.4 mg (mean ± SD = 74 ± 117 mg). The minimum and maximum values of the size distribution correspond to a juvenile *Tetragnatha* and an adult female *Araneus* sp. respectively. We performed these trials in four different blocks (four weekends in summer 2003). All trials were performed at room temperature in the laboratory. Spiders were encouraged to run on a vertical rod (1.20 m high, 3 cm in diameter) in a different manner depending on the species (see also Moya-Laraño *et al.*, 2007b). Individuals of *L. venusta* (Tetragnathidae), for example, were placed on top of the rod (on the 3-cm-diameter surface) and gently pushed 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 the race, the only attaching points for climbing were on the rod itself. Other spiders (e.g. Thomisidae) were just placed at the base of the pole and we waited until they started climbing. For each trial, we measured the starting and ending points of a continuous spider race (> 10 cm) and used a stopwatch for timing. In order to improve timing accuracy, one of us handled the spider, whereas the other handled the stopwatch. To analyse the data, we used a general linear mixed model (GLMM) in which both the taxon (family) and the block (weekend) effect were entered as random factors. Moreover, we analysed the data using a generalized least squares model (GLS) that incorporates phylogenetic relationships (see below) to correct for nonindependence due to common ancestry (reviewed Garland *et al.*, 2005). The GLS analysis was implemented in R using the package PHYLOGR (Diaz-Uriarte & Garland, 2007). The response (speed) was modelled as a function of size, while controlling for the variance–covariance matrix of phylogenetic distances and for block effects (weekend), which were included as dummy variables. As different instars of different species were included and genitalia are not present in the juvenile instars, which makes identification unfeasible, we decided to include within the phylogeny all the individuals from the trials. Individuals belonging to the same genus were included as polytomies. To handle differences in the scale of measurement, we log transformed both climbing speed (cm s^{-1}) and body mass (mg). Prior to log transformation, we took the cubic root of body mass to make it linearly comparable with speed and to conform to the prediction of the GH that a negative relationship exists between climbing speed and any proxy of body length (L). Both in the GLMM and in the GLS models, we incorporated quadratic terms for the mass component in the model to test if there was an optimal body size for climbing. GLS analysis is the most appropriate phylogenetic comparative method to accomodate nonlinear relationships (Quader *et al.*, 2004). To visualize this pattern, we drew a partial residual plot, which is the most appropriate to graphically depict curvilinear patterns (Moya-Laraño & Corcobado, 2008). First, we ran a GLMM model including block, family and the linear effect of mass. From this model, we extracted the residuals and added the predicted speed value from the linear effect of mass in the model, creating a new variable which we called Y residual. The partial residual plot was obtained by plotting Y residual against mass. If a quadratic term needs to be fit to the overall model, and thus an optimal climbing speed is detected, the partial residual plot will show a clear curvilinear trend (see Moya-Laraño & Corcobado, 2008 for details on this technique). If a curvilinear pattern was detected, we determined the mass value at which climbing speed is optimal by calculating the first derivative of the quadratic model.

Comparative analyses

As our climbing trials revealed an optimal size for climbing speed at approximately 43 mg body mass (≈7.4 mm body length; according to Edwards, 1996 equation for a wide range of spider taxa; see the Results section), we predicted that in species that live in high-habitats males should not evolve beyond this optimal size and hence pronounced SSD should become apparent with increasing size of the females – in contrast to species that live on the ground where male size is predicted to co-evolve tightly with female size, as running speed on horizontal surfaces typically increases with size (Bauwens *et al.*, 1995; Brandt & Andrade, 2007a; Moya-Laraño *et al.*, 2008). To test this prediction, we used the data set from Moya-Laraño *et al.* (2002). We collapsed the original grouping (i.e. four habitat height ranks that were obtained from habitat descriptions in the literature; ranging from the lowest to the highest: 1 – soil or litter, 2 – low grass, 3 – tall herbs or bushes and 4 – trees or cliffs) into two categories (low-habitat: ranks 1 and 2 vs. high-habitat: ranks 3 and 4). Regression analyses using the 'tips' data, i.e. ln(male length) on ln(female length), for high- and low-habitat spiders have been published separately (Foellmer & Moya-Laraño, 2007). Here, we conducted a phylogenetically controlled comparative GLS analysis in R using PHYLOGR (Diaz-Uriarte & Garland, 2007). A total of 107 species from 25 families and 75 genera were included in the analyses.

Phylogenetic relationships

We updated species classifications following the World Spider Catalogue (Platnick, 2008) and used PDAP v. 6.0 (Garland *et al.*, 1992, 2005) to obtain the phylogenetic variance–covariance matrices for the GLS analyses based on the current knowledge of spider phylogeny (Scharff & Coddington, 1997; Maddison & Hedin, 2003; Agnarsson, 2004; Arnedo *et al.*, 2004; Benjamin, 2004; Coddington, 2005; Murphy *et al.*, 2006). Phylogenetic trees were first built in PDTREE and then saved as matrices in PDDIST (Diaz-Uriarte & Garland, 2007). Taxonomy was assumed to reflect phylogeny; hence, unresolved nodes were entered as polytomies. That is, if no other information was available, all genera descended from the common family node and all species from the common genus node. As estimates for branch lengths were not available, we set all branch lengths arbitrarily equal to 1 (Diaz-Uriarte & Garland, 1998).

Results

Climbing trials

The model showed a clear curvilinear pattern for the relationship between body size and climbing speed, with block but not family significant effects (Table 1). The partial residual plot showed this pattern as well (Fig. 1). The derivative analysis estimated the optimal body size to be 43.2 mg, which corresponds to about 7.4 mm of body length (Edwards, 1996). A phylogenetically controlled GLS analysis showed a significant curvilinear pattern (Table 1). This model predicted an optimal body mass of

Table 1 Statistical models on the effect of mass on climbing speed across spiders.

Variable	Estimate	SE	d.f. num	d.f. den	*F*-value	*P*
GLMM						
Intercept	1.6	0.5	1	55	25.4	0.001
Block*			3	55	4.2	0.010
Family†			4	55	0.6	0.669
Mass	**1.2**	**0.4**	**1**	**55**	**9.0**	**0.004**
Mass^2	**–0.5**	**0.2**	**1**	**55**	**7.2**	**0.010**
Variable	Estimate	SE	d.f.		*t*-value	*P*
GLS						
Intercept	1.3	0.6	59		2.1	0.043
Block 1	0.4	0.4	59		1.0	0.300
Block 2	0.4	0.4	59		1.0	0.294
Block 3	0.2	0.5	59		0.4	0.661
Mass	**1.1**	**0.4**	**59**		**2.7**	**0.008**
Mass^2	**–0.4**	**0.2**	**59**		**–2.3**	**0.028**

Coefficients relevant to the gravity hypothesis are expressed in bold.
*Block refers to different groups of trials each of which was conducted on a different weekend.
†Family refers to one of the next taxonomical spider families: Araneidae, Pholcidae, Tetragnathidae, Theridiidae or Thomisidae.

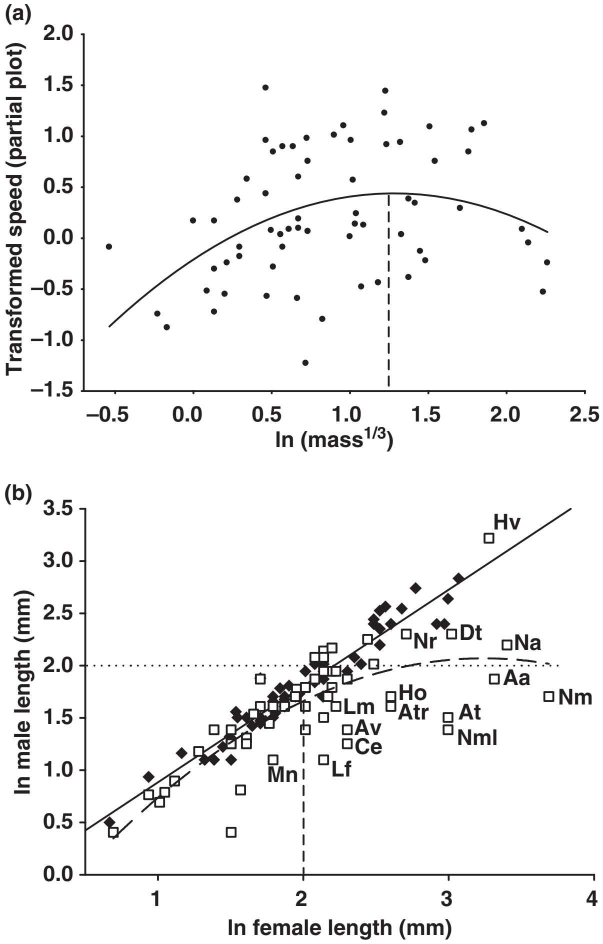

Fig. 1 Empirical test of the gravity hypothesis and the influence of the (curvilinear) pattern on spider sexual size dimorphism (SSD). (a) Partial residual plot showing the relationship between log body size (mass) and log climbing speed in spiders (model in Table 1). The dashed vertical line shows the optimal body mass for climbing (≈43 mg). This relationship predicts a curvilinear pattern of SSD in spiders from tall habitats. (b) The linear and curvilinear patterns of SSD in short-habitat spiders (black diamonds and solid line) and tall-habitat spiders (white squares and dashed line) respectively. The horizontal dotted line and the vertical dashed line, respectively, show the male and female body lengths which correspond to the optimal climbing speed (≈7.4 mm). Note how 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 all species but one (Hv) present males of size which fluctuate around the threshold (horizontal dotted line). Note that spiders from distant taxa are responsible of the curvilinear pattern: Araneidae (Aa, *Argiope aemula*; At, *A. trifasciata*; Av, *A. versicolor*, Atr, *Araneus trifolius*; Ce, *Cyrtophora exanthematica*; Nr, *Neoscona rufofemorata*), Nephilinae (Lf, *Leucauge fastigiata*; Ho, *Herennia ornatissima*; 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 a clear outlier (Hv, *Heteropoda venatoria*). Panel (b) redrawn from Foellmer & Moya-Laraño (2007), with permission of Oxford University Press.

43.3 mg, suggesting that the approximate true optimal mass for climbing is approximately 43 mg.

Comparative analyses

The GLS analysis shows that the relationship between male and female size (body length) differs between the high- and low-habitat spiders (see Fig. 1b for a display of the tips). Low-habitat species exhibit a linear relationship [GLS: $\ln(\text{male body length}) = -0.02 + 0.98 \ln(\text{female body length})$; $P < 0.0001$; quadratic term; $P = 0.481$]. High-habitat spiders show a nonlinear relationship, and the curvilinear trend starts very close to the female threshold, as predicted by the pattern of climbing speed [GLS: $\ln(\text{male body length}) = -0.80 + 1.73 \ln(\text{female body length}) - 0.27 \ln(\text{female body length})^2$; both the linear and quadratic mass terms were significant: $P < 0.0001$ and 0.001, respectively, and there were no block effects, all $P > 0.34$]. Note that we removed an outlier species *Heteropoda venatoria* (see the Discussion section for an explanation).

Discussion

Our results suggest that SSD in spiders has evolved according to the climbing abilities conferred by different body sizes, because extreme SSD has evolved only in those species in which: (a) males have to climb to find females and (b) females are larger than the optimal climbing mass. We found that when considering a wide range of spider body sizes, there is an optimal mass of 43 mg (7.4 mm) for climbing at which climbing speed is maximum (i.e. 10.2 cm s^{-1}) and that this optimal body size predicted the pattern of SSD in spiders that live in high habitats. In spiders that live at ground level, in which males do not have to climb to reach females, male and female sizes follow a perfect linear pattern in a log–log plot. However, in species in which males have to climb to reach females, the pattern is linear up to the threshold of 7.4 mm for female size and becomes curvilinear after that, thus demonstrating decoupled evolution of male and female size. The GLS analyses revealed that these patterns held even after controlling for common ancestry. The GH (Moya-Laraño *et al.*, 2002) predicted a negative relationship between climbing speed and body size. Our analysis using a wide range of body sizes demonstrated no negative relationship, but a curvilinear one, showing an optimal body size for climbing.

Contrary to previous studies (e.g. Brandt & Andrade, 2007a), in our trials we sought to use as wide a range of body sizes as possible, and a curvilinear optimal climbing speed was evident even after controlling for common descent. Here, we have also used the comparative method to test whether the optimal climbing speed at which spiders climb predicts the evolution of SSD. The evolutionary prediction behind the GH is that due to the body size constraint, smaller males will be favoured by selection during mate search, something that needs to be tested studying natural selection in the wild (as the field examples in Table 2). In addition, to prevent potential pseudo-replication in the current study; e.g. that the hypothesis could work only in a particular spider group that would inflate the degrees of freedom of the test, we included spider family as a random block effect in the GLMM analysis of climbing trials and also confirmed the pattern using a phylogenetically controlled GLS analysis. Thus, despite arguments by some authors (Brandt & Andrade, 2007b), it is unlikely that our analysis suffers from any major flaw.

We found that when females are larger than the threshold for optimal climbing speed (vertical dashed line), in all high-habitat species but one (*H. venatoria*), male size remains close to the threshold of maximum climbing size (horizontal dotted line) (Fig. 1b). This contrasts with low-habitat species, in which the relationship between male and female body sizes is linear.

Table 2 Summary of studies that directly or indirectly tested the gravity hypothesis using males of species with extreme SSD.

Species	Family	Mass range (mg)	Mass difference (mg)*	Type of study	Evidence for GH	Reference
Latrodectus hasselti	Theridiidae	0.6–10	–33	Field†	No	Andrade (2003)
Latrodectus hesperus	Theridiidae	6–27	–16	Laboratory	No	Brandt & Andrade (2007a,b)
Argiope aurantia	Araneidae	11–31	–12	Field	No	Foellmer & Fairbairn (2005)
Nephila plumipes	Tetragnathidae	14–23‡	–20	Field	No	Kasumovic *et al.* (2007)
Nephila clavipes	Tetragnathidae	6–65	22	Field	Yes	Linn (2001)
Leucauge venusta	Tetragnathidae	8–13	–30	Laboratory	No	Moya-Laraño *et al.* (2007b)
Nephila clavipes	Tetragnathidae	6–65§	22	Field	Quadratic¶	Vollrath (1980)

*This value indicates the difference between maximum male mass and the optimal body mass for climbing (43 mg).

†Field study usually involves marking and release of individuals, or similar procedure.

‡As mass range was not provided in the original study, we obtained it from table 6 in Schneider & Elgar (2002).

§As body mass for this study was not available, we include here the range in Linn (2001).

¶The pattern was quadratic, with males of intermediate size having a higher chance to reach females (see text for a re-analysis of these data).

Heteropoda venatoria is a clear outlier which, like all Sparassidae, has a very flat body, lateral legs and abundant fine hair (scopulae) that has been demonstrated to function to enhance adhesion to smooth vertical surfaces (Niederegger & Gorb, 2006), suggesting that this species may be highly adapted to climb. Alternatively, other modes of locomotion could be responsible for the observed pattern of SSD. Males do not only climb to reach females in high habitats, they also bridge (among other dispersal modes, e.g. walking). For bridging, spiders release a silk line downwind that they tense as soon as it attaches to an opposite end (e.g. a twig) and cross it by walking upside down underneath the silk line (Peters, 1990). This dispersal mode has been shown to take advantage of pendulum mechanics (Moya-Laraño *et al.*, 2008). Whether a relatively small size also could be advantageous during bridging remains to be investigated.

In most of the previous tests of the GH, maximum male mass was well below the threshold mass allowing maximum climbing speed (Table 2). In fact, the only study that supported the GH (Linn, 2001) included male masses that expanded beyond the threshold. We found that this trend was significant in a logistic regression analysis in which the difference between male maximum body mass and the threshold was included as the independent variable (values in Table 2) and evidence for the GH (yes/no) as the dependent variable ($\chi^2 = 5.4$, 1 d.f., $P = 0.02$). In addition, the only convincing test demonstrating a negative relationship between climbing speed and body mass was performed with females (Moya-Laraño *et al.*, 2007b), which greatly expanded the mass range beyond the threshold (mass range 10–87 mg). This test was carried out to expand the range beyond that of males. Thus, the current evidence seems to be consistent with an optimal size for climbing rather than with a mere negative relationship between climbing speed and body size. Interestingly, another study in which the range of spiders expanded beyond the threshold for optimal climbing (Vollrath, 1980) found that males of intermediate size were more probably recaptured on a second female web; however, no formal statistical analysis was reported in the original publication. We re-analysed Vollrath's (1980) data set (his table 2) and found that indeed the intermediate category of male size had a higher probability of being recaptured on a second female web (logistic regression, linear term: $\beta = 4.8$, $P = 0.003$; quadratic term: $\beta = -1.0$, $P = 0.006$; $n = 532$). Therefore, in species with sufficient size spread, stabilizing selection for an optimally climbing body size may be at play. In addition, this is reinforced by the fact that one of the studies in which males are way below the optimal body size (Foellmer & Fairbairn, 2005) showed a large male advantage during mate search.

The original GH already predicted that SSD would be more pronounced in larger species that live in high places (Moya-Laraño *et al.*, 2002). However, our climbing trials using a wide range of body sizes allowed us to clearly see the nature of such an interaction; there is a linear pattern of SSD for species that live at ground level and a curvilinear pattern for species that live in tall places. One important conclusion that we can make is that the original biomechanical model of the GH (Moya-Laraño *et al.*, 2002) does not grasp the true relationship between climbing speed and body size. Below, we develop a biomechanical model that explains this curvilinear pattern of optimal climbing.

Explaining the curvilinear climbing pattern: an *ad hoc* biomechanical model

Muscles are under a constant external force F during climbing because they have to lift the body during the entire time of contact with the surface (Goldman *et al.*, 2006). This is very different from horizontal walking where muscles have to lift the body only for a fraction of contact time. Therefore, the total (sum over all legs) average force on muscles during climbing is the body weight, $F = mg$ (m is body mass and g is the acceleration of gravity) (Goldman *et al.*, 2006). For comparison, horizontal walking requires only a fraction of that force on average (Full *et al.*, 1991). Although in reality legs differ in their dynamical properties during climbing, the sum of forces over all legs should follow the above model.

In the following analysis, we assume that all variables are averaged over a stride period. The mechanical power output of a muscle is defined as the rate of kinetic work $P_{\text{out}} = Wf = F\Delta lf$, where $W = F\Delta l$ is the work output of a muscle during one stride and Δl is the muscle contraction distance. Since overall muscle length scales with leg length L_{leg}, we can assume $\Delta l \propto L_{\text{leg}}$ (Shultz, 1989). Body speed, v, is a product of a stride length and stride frequency f. In geometrically similar animals, stride length scales with leg length L_{leg}, which gives:

$$v \propto L_{\text{leg}} f \tag{1}$$

Combining all these variables together yields the mechanical power output of climbing:

$$P_{\text{out}} \propto m L_{\text{leg}} f \propto L^3 L_{\text{leg}} f \propto L^3 v \tag{2}$$

where mass scales as volume L^3. The same scaling equation was derived by Moya-Laraño *et al.* (2002), but from gravitational potential energy arguments. In order to climb a height difference h during time t, an animal has to produce muscle work equivalent to the gravitational potential energy difference $W = mgh$. From $P_{\text{out}} = W/t$ it follows that $P_{\text{out}} = mgh/t = mgv$. This relationship showing that P_{out} in climbing is different from biomechanics of walking on flat surfaces has been demonstrated in the gecko *Hemidactylus garnotii* (Autumn *et al.*, 2006).

The derived mechanical power *output* has to be compared with metabolic power *input*, which is actually relevant in the adaptive evolution of body size (Peters, 1983). However, it is difficult to analytically estimate metabolic power because many factors affect the work output from muscles: stride frequency, muscle contraction length, rate and trajectory (e.g. sinusoidal and triangular), the pattern of muscle stimulation and muscle temperature among others (Josephson, 1993). Experimental measurements of metabolic mass-specific power input of horizontally walking or running terrestrial animals can be approximately described by (e.g. Taylor *et al.*, 1982):

$$\frac{P_{\mathrm{in}}}{m} = Tv + P_0 \tag{3}$$

where the slope T is the minimum metabolic cost of transport and P_0 is the resting metabolic rate that describes a motionless body in an erect position ready to start moving. Data for horizontally walking and running animals of various species in mass ranges from about 10 mg to 100 kg can be approximated by $T = 10.7m^{-0.32}$ and $P_0 = 6m^{-0.30}$, where mass is in kg, speed in m s^{-1} and power in W kg^{-1} (Peters, 1983; Full & Tu, 1991; Alexander, 2003). This relationship revealed that larger animals are more efficient during horizontal walking.

Unfortunately, there is no similar empirical relationship for climbing. It may also not be possible to have a very general relation considering that climbing critically depends on body design and the ability to attach to a vertical surface. For example, biomechanical analyses of geckos and monkeys (Hirasaki *et al.*, 2000; Zaaf *et al.*, 2001) show how differences in body design can improve climbing abilities. Observations show that insects optimized for horizontal walking tend to maintain geometrical similarity between horizontal and inclined walk (Lipp *et al.*, 2005; Goldman *et al.*, 2006). Thus, the metabolic cost of climbing is increased mostly due to the investment of energy into larger muscle forces needed for lifting the body. If eqn 3 represents a viable approximation of the metabolic cost of climbing, or at least its most rudimental approximation, then a few existing measurements of walking on inclines for invertebrates (Full & Tullis, 1990; Roberts *et al.*, 1997; Wickler *et al.*, 2000; Lipp *et al.*, 2005) suggest that the second term in eqn 3 dominates the metabolic power (for simplicity, we approximate $m^{-0.30}$ with $m^{-1/3}$):

$$P_{\mathrm{in,climb}} \propto m^{2/3} \propto L^2 \tag{4}$$

where L is body size (length).

If spiders of different size maintain a geometric similarity of their muscle work cycles, then they also maintain the efficiency of transforming metabolic into mechanical energy $P_{\mathrm{in,climb}} \propto P_{\mathrm{out}}$, which gives (eqns 2 and 4):

$$v \propto \frac{1}{L} \tag{5}$$

This result was also derived by Moya-Laraño *et al.* (2002) who assumed eqn 4 without a detailed analysis. According to eqn 5, a smaller size leads to a higher speed of climbing, even though our suggested metabolic power in eqn 4 is independent of climbing speed. The consequence is that muscles will operate at a work cycle that maximizes the speed while producing enough power output for lifting the body. According to muscle physiology, an increase in muscle tension force leads to a smaller muscle contraction speed and vice versa (Hill, 1938; Josephson, 1993). Muscles during climbing have to support the body weight $mg \propto L^3$, which produces muscle tension scaled as $mg/L^2 \propto L$. Hence, reducing body size results in a smaller muscle tension, which in turn increases muscle contraction speed, i.e. climbing speed.

The maximum speed limit must be set by muscle physiology because the speed in eqn 5 should not go to infinity as the size goes to zero. There has to be some physical limit to this trend. Equations 1 and 5 imply that stride frequency grows very fast with a decreasing spider size ($f \propto 1/L_{\mathrm{leg}}L$). Muscles can operate efficiently only up to a certain frequency above which the mechanical work output decreases rapidly (Stevenson & Josephson, 1990; Josephson, 1993). Hence, for smaller spiders stride frequency has to deviate from eqn 1. If it is reduced to:

$$f \propto \frac{1}{L_{\mathrm{leg}}} \tag{6}$$

then speed (eqn 1) becomes constant. For even smaller spiders, stride frequency becomes constant by reaching its physiological limit, whereas the speed is:

$$v \propto L_{\mathrm{leg}} \tag{7}$$

At this point, the assumptions made about the metabolic cost of climbing in eqn 4 cannot be maintained and the metabolic cost of climbing becomes similar to horizontal walking described by eqn 3.

Equations 5–7 describe three different regimes of climbing (Fig. 2) that have to be empirically tested. It is

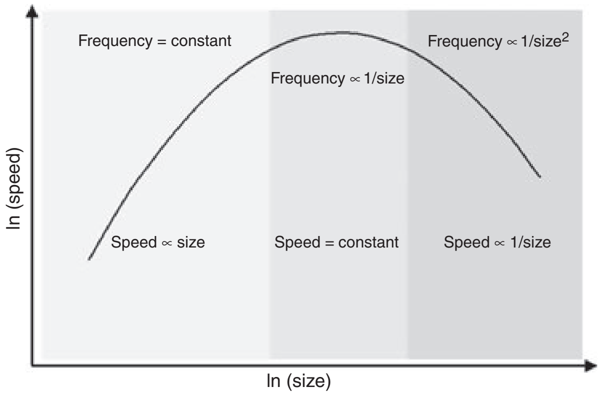

Fig. 2 Climbing speed depends on size over roughly three regimes as marked in this sketch. Our theoretical model shows that the same holds for stride frequency because speed ∝ size × frequency (see text for details).

interesting that measurements of metabolic rates in ants (mass < 43 mg) show the exact trend of $f =$ constant regime (Lipp *et al.*, 2005), whereas in much larger cockroaches (mass > 43 mg) measurements are consistent with a $f \propto 1/L^2$ regime (Full & Tullis, 1990). We provide a more comprehensive observation based on measurements of climbing speed in spiders of different sizes. Below a calculated threshold of 43 mg, larger spiders climb faster, consistent with $f =$ constant; whereas above that threshold larger spiders tend to climb at a lower speed, consistent with $f \propto 1/L^2$. Thus, although the hypothesis of a change in the frequency of stride needs to be tested with detailed measurements (e.g. with high speed cameras), so far results are consistent with it.

There are conspicuous differences in shape among spider groups that can explain their climbing ability (e.g. see the case of *Heteropoda*, above). Differences in climbing ability among spider groups are probably explained by the obvious morphological differences existing among them (e.g. leg length and diameter, distance from the body to the climbing surface and lateralization of legs). Thus, any statistical analysis comparing data from different spider species has to take also into account that some spiders are more adapted than others to walk on inclined surfaces. Differences in climbing ability among spider groups were partially taken into account when analysing the results of the present study by entering the spider taxon family as a random factor in a GLMM and by taking into account the phylogeny in a GLS. However, the role of shape should be considered in future studies including measures of morphological differences.

Conclusions

We have extended the GH to accommodate a curvilinear pattern of climbing with an optimal body size that determines maximum climbing speed. This threshold body size successfully explains when extreme SSD is expected to evolve in spiders that live in high-habitat patches, and thus when the evolution of male and female body sizes should be decoupled. Studies failing to support the GH include males that are well below the threshold body size, one of them even finding that large males are favoured. This indicates that other species-specific selection pressures probably operate in those systems keeping males at a small size. Thus, to better understand SSD, these specific pressures should be investigated in the future. However, we predict that studies with species in which males have a size span beyond the threshold will show evidence for the GH. Finally, we present a biomechanical model explaining the optimal body size for climbing according to body size limitations in stride frequency. High-speed camera experiments should be used to test this model. We believe that this study provides a framework for future studies on SSD.

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