

Gravity still matters

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Several factors may influence the evolution and maintenance of sexual size dimorphism (SSD) in spiders (reviewed in Foellmer & Moya-Laraño 2007). Although the fecundity selection hypothesis (Gerhardt 1924; Head 1995; Hormiga *et al.* 2000) successfully explains the evolution of female gigantism, this hypothesis cannot successfully explain why in some spiders males are barely smaller than females while in others males are substantially smaller than females. This high variation in SSD is in need of explanation. The most recent hypothesis that has been put forward to explain this large variation in SSD in spiders is the gravity hypothesis (GH) (Moya-Laraño, Halaj & Wise 2002), which focuses on the adaptive significance of small male size (relative to female size). The interest of this hypothesis lies in the fact that other hypotheses that attempt to explain relative small male size in spiders are either of limited applicability or have been refuted (reviewed in Foellmer & Fairbairn 2005; Foellmer & Moya-Laraño 2007). In addition, clear demonstrations of the advantages of small body size are generally rare in animals (reviewed in Blanckenhorn 2000; Blanckenhorn 2005), and thus there is a need for hypothesis development and further testing in this area.

The GH 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). It predicts that males of small size should have an advantage during mate search in species where males have to climb to reach females, which is the case in many spider species that inhabit three-dimensional habitats such as old fields or forests (Moya-Laraño *et al.* 2002). Small males should be better at escaping predators and/or reaching females faster than larger males, leading to an advantage in scramble competition (Moya-Laraño *et al.* 2002). In addition, the GH predicts that female-biased SSD is likely to be more pronounced in species where females build their webs high up in the vegetation than in species where females place their webs closer to the ground (Moya-Laraño *et al.* 2002).

A recent paper by Brandt & Andrade (2007) about climbing patterns in the male theridiid, *Latrodectus hesperus* did not support the GH. The authors argued against the biomechanical model of the GH and presented a model that claimed that mechanical force and not power, as assumed by the biomechanical model in Moya-Laraño *et al.* (2002), is proportional to the muscle cross-sectional area. Under this assumption, climbing speed is predicted to be independent of body size, as Brandt & Andrade (2007) found for male *L. hesperus*. The authors found that on flat surfaces, larger *L. hesperus* males ran faster and, based upon these results, proposed a new hypothesis to explain the patterns of SSD found by Moya-Laraño *et al.* (2002): on flat surfaces, males are similar in body size to females because selection favours large male body size during mate searching; however, on vertical surfaces, there are no selection pressures favouring large male body size, and protandry selection (i.e. selection to mature earlier at a smaller size for early access to receptive females) drives small male body size.

Below we respond to Brandt & Andrade's (2007) criticisms of the biomechanical model in Moya-Laraño *et al.* (2002). First, we identify important inconsistencies and flaws in their alternative model, thereby showing that it cannot adequately describe the biological processes involved. Second, we show how their alternative explanation for the pattern found by Moya-Laraño *et al.* (2002) is unsupported by the current evidence. Third, we provide several alternative hypotheses to explain the apparent lack of a relationship between climbing speed and body size found by Brandt & Andrade (2007) for male *L. hesperus*. Finally, we concede that given the current state of knowledge about locomotion in small animals and how it is affected by size, it is probably too early to reach firm conclusions, but we wish to emphasize that the GH and its underlying biomechanical model are internally consistent and are supported by the published literature on climbing performance and the physiology of muscle operation.

Here we show how several of the main points in Brand & Andrade's alternative biomechanical model are misleading. First, we stress that the biomechanics of climbing are very different from the biomechanics

of walking or running on flat surfaces. As explained in the original publication (Moya-Laraño *et al.* 2002), when an animal has to climb, it has to produce enough mechanical power (i.e. work per unit of time, $P = W/T$) to overcome the potential energy imposed by gravity ($E = mgh$), which when translated into the necessary power output to climb height h we get the equation,

$$P = mgv \quad \text{eqn 1}$$

where v is climbing speed. The assertion that the biomechanics of climbing follows this relationship and is therefore different from the biomechanics of walking on flat surfaces has been demonstrated in the gecko *Hemidactylus garnotii* (Autumn *et al.* 2006). If we then consider the basic assumption of Brandt & Andrade (2007) that force, not power, is proportional to the muscle cross-section area and since by definition power is equal to the rate of work (work/time), we get

$$P = Fv \quad \text{eqn 2}$$

That is, power output equals force times velocity. If we now take eqns (1) and (2) we get the following:

$$F = mg \quad \text{eqn 3}$$

Since m is proportional to L^3 and, according to Brandt & Andrade, force is proportional to L^2 , we get that L^2 would be proportional to L^3 . This is an unphysical statement and thus incorrect. Hence, Brandt & Andrade's (2007) model cannot adequately explain the biomechanics of climbing. In addition, the assumption that force scales with the muscle cross-section is not realistic. In reality, muscles activate a different percentage of their fibres according to the external force, and this flexibility allows muscles to adjust to the different weight loads during movement (Taylor *et al.* 1980). Therefore, the assumption that the number of active fibres is proportional to the muscle cross-section is not valid. Putting this in the context of climbing is straightforward: an animal that is too heavy will exert maximum force for climbing, but it may not move because the force may not be enough to overcome gravity. In this situation, force would be the maximum while speed (and thus power output) would be zero.

Other internal inconsistencies are patent in Brandt & Andrade's model. The muscle work is described as the force produced by a muscle during its contraction by distance Δl :

$$W = F\Delta l \quad \text{eqn 4}$$

When Brandt & Andrade made the assumption that force is proportional to the muscle cross-sectional area, they argued that the total mechanical force on a muscle comes from a sum of individual muscle fibres, where the number of muscle fibres is proportional to the muscle cross-sectional area. They conclude that this

yields $P \propto L^3 \propto M$ (where L and M are body size and mass, respectively) because the muscle cross-sectional area scales as L^2 and Δl scales as L . Hence, mass-specific power P/M is independent of body size. They compare this with the mechanical mass-specific power of climbing $P/M \propto \text{speed}$ derived by Moya-Laraño *et al.* (2002) and conclude that size has no effect on maximal vertical climbing speed. Another objection to this model is the omission of time T in the conclusion that $P \propto L^3$. They assume that $F \propto L^2$ and $\Delta l \propto L$, which yields $W \propto L^3$ from eqn 4. In order to obtain $P \propto L^3 \propto W$, we have to assume that $1/T$ in $P = W/T$ is constant. Since the underlying assumption in this theoretical analysis is that all variables are averages over stride duration, we can set T to be a stride period and see that Brandt & Andrade (2007) assumed a constant stride frequency $f = 1/T$. This leads to a problem with their model; speed v is a product of stride length and stride frequency, where stride length scales with L , and therefore:

$$v \propto Lf \quad \text{eqn 5}$$

If speed is constant, then $f \propto 1/L$, which contradicts the basic assumption of constant f used in deriving $P \propto W$.

All these arguments demonstrate that the analytical model in Brandt & Andrade (2007) is not adequate for explaining the physics of climbing arthropods. Even if the assumption that during climbing force is proportional to the muscle cross-sectional area holds, the inclusion of muscle contraction speed (a surrogate of stride speed) into the picture would support the original model of Moya-Laraño *et al.* (2002). The force produced per muscle cross-section has been shown to be constant across a wide range of body sizes and animal taxa (Medler 2002), and, in addition, smaller animals have been shown to have higher muscle contraction speed. Since there is also a correlation between contraction speed and muscle force (Medler 2002), we can see how lighter animals will be able to contract their muscles at a higher speed, scaling as -0.125 (following Medler 2002) and thus contraction speed is proportional to $L^{-0.375}$. Now, considering eqn 2 and the fact that force is proportional to the muscle cross-sectional area, we can see how muscle power output would be proportional to $L^{1.625}$ and therefore much closer to L^2 (as in Moya-Laraño *et al.* 2002) than to L^3 (as derived by Brandt & Andrade 2007). Thus, if we consider stride speed, the fact that muscle force is proportional to L^2 does not invalidate the assumption in Moya-Laraño *et al.* 2002. If anything, the value is lower, which would change the main prediction from v proportional to L^{-1} to v being proportional to $L^{-1.325}$. However, the exact value of these coefficients should not matter, since they would be likely to change depending on whether the animal is walking, climbing or running, and also depending on body shape. We must stress that these are just approximations and that we know very little about the physiology of climbing, particularly in small organisms. Moreover, spider

movement does not only depend on muscle operation but also on hydrostatics, since, as acknowledged by Brandt & Andrade (2007), leg extension depends on the pumping of haemolymph from the body into the legs (Foelix 1996). Thus, leg length and diameter (i.e. the diameter of the pipe in which liquid is being pumped), and extrinsic pumping muscles (within the carapace) must play a relevant role in spider movement that is yet to be investigated.

There is a much simpler way to describe the GH. For a fixed amount of maximum power input, the running or walking power output, and thus the achievable speed, will diminish with weight load to a higher degree on a vertical surface than on a horizontal surface. One solution for an animal that has to climb is to be relatively smaller (i.e. to carry relatively less weight) than the animals that do not have to climb. This simple approach explains the pattern of SSD in spiders very well. First, SSD is much stronger for body length or body mass than for carapace width (Foellmer & Moya-Laraño 2007), indicating that the strongest selection has been to shrink the abdomens of the males in order to decrease weight load. This must be particularly important in species with large females that live in habitats high off the ground, since fecundity selection is likely to have selected not only for an overall large size in females but also for a maximum abdomen expandability so as to hold as many eggs as possible. Interestingly, the cases of extreme SSD appear mostly in species with relatively large females that live in relatively high places (Moya-Laraño *et al.* 2002; Foellmer & Moya-Laraño 2007). Ironically, the prediction of the GH that weight load decreases climbing speed has been demonstrated in one of the lizard papers cited by Brandt & Andrade (2007), which they used to support the point that smaller lizards do not climb faster (Isrckick *et al.* 2003). At least in spiders, future work should focus on traits determining running performance (e.g. carapace width, leg length and leg diameter), and then study how these traits scale with body mass and how locomotion is affected by these variables across a broad range of taxa/body sizes. In addition, we would like to emphasize that the fact that smaller animals have higher muscle forces and higher stride speed (Medler 2002) adds a new interesting twist to the whole story, since a small animal could compensate its shorter step lengths with faster leg movement.

The alternative hypothesis of Brandt & Andrade (2007) (i.e. males of species that live in high habitats are smaller than females because there is no selection favouring larger males) does not explain the second prediction of the GH, that the effect of gravity should be stronger on larger species (or taxa). This was strongly supported by the comparative method in the original paper by showing that there is a significant interaction between habitat height and female body size explaining SSD (Moya-Laraño *et al.* 2002). These authors also argue that the pattern of stronger SSD in spiders that live in high habitats, as found by Moya-Laraño

et al. (2002), could be explained by differential female gigantism (i.e. by stronger fecundity selection on females that live in high habitats relative to females that live at ground level). However, the authors did not realize that the analyses in Moya-Laraño *et al.* (2002) did include female body size as a covariate in the analysis, which completely ruled out the possibility of differences on selection in female size having an influence on the pattern. Furthermore, their alternative hypothesis relies on a male advantage from protandry selection, which is yet to be demonstrated to operate in spiders (Foellmer & Moya-Laraño 2007). A potential explanation for why Brandt & Andrade (2007) did not find the negative relationship between climbing speed and body size predicted by Moya-Laraño *et al.* (2002) is that in their trials, there was not enough variation in male body size for gravity to have an effect on climbing speed. By using a much wider range of spider sizes, we have found that there is an optimal body size for climbing at 42.5 mg (roughly 7.6 mm) (Foellmer & Moya-Laraño 2007), suggesting that for small body sizes, the physics of climbing is different from that of large body sizes. The size range of males used by Brandt & Andrade is 3–6.5 mm, well below the threshold for which a negative relationship between climbing speed and body size arises empirically. Why the negative relationship between body size and speed did not arise when using data for a single sex is intriguing. However, we must distinguish between the evolution and the maintenance of a trait. Indeed, the GH explains that the strong pattern of SSD found in spiders that live in tall places was originated by selection acting against large male body size because smaller males would have a climbing advantage. A possible explanation for the lack of a pattern within males alone is that in species with pronounced SSD, this dimorphism was fixed some time during their evolutionary history (when it was adaptive according to the GH) 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. However, the maintenance of the patterns of SSD may largely depend on a completely different set of environmental factors. Although selection against large body size may be ongoing, the effect is likely to be so small and fluctuating that it remains largely undetected for the sample sizes that are logistically achievable in this type of experiment.

In conclusion, we have shown how Brandt & Andrade's (2007) alternative biomechanical model and alternative hypotheses to the GH are far from supported by the current evidence and we have also shown additional theoretical support for the GH.

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