DISCUSSION

Energetics, Scaling and Sexual Size Dimorphism of Spiders

B. Grossi · M. Canals

Abstract The extreme sexual size dimorphism in spiders has motivated studies for many years. In many species the male can be very small relative to the female. There are several hypotheses trying to explain this fact, most of them emphasizing the role of energy in determining spider size. The aim of this paper is to review the role of energy in sexual size dimorphism of spiders, even for those spiders that do not necessarily live in high foliage, using physical and allometric principles. Here we propose that the cost of transport or equivalently energy expenditure and the speed are traits under selection pressure in male spiders, favoring those of smaller size to reduce travel costs. The morphology of the spiders responds to these selective forces depending upon the lifestyle of the spiders. Climbing and bridging spiders must overcome the force of gravity. If bridging allows faster dispersal, small males would have a selective advantage by enjoying more mating opportunities. In wandering spiders with low population density and as a consequence few male–male interactions, high speed and low energy expenditure or cost of transport should be favored by natural selection. Pendulum mechanics show the advantages of long legs in spiders and their relationship with high speed, even in climbing and bridging spiders. Thus small size, compensated by long legs should be the expected morphology for a fast and mobile male spider.

Keywords Cost of transport · Dimensional analysis · Selective pressure · Spiders

1 Introduction

The extreme sexual size dimorphism in spiders (SSD) has motivated studies for many years. In many species the male can be very small relative to the female. This

B. Grossi · M. Canals (✉)
Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Santiago, Chile
e-mail: mcanals@uchile.cl

could be explained by selection for large female size, small male size, or both. There is good evidence that fecundity selection in females favoring large size (fecundity advantage hypothesis) is one of the main factors contributing to the evolution and maintenance of sexual SSD (Foellmer and Moya-Larraño 2007; Santos 2007), mainly mediated by a strong correlation between female body size and clutch size (Head 1995). Hypotheses to explain the selection of the body size of the male are included in some of the following premises: (1) where population densities are low, there is relaxing of selection for large male size (due to male–male interference) (Ghiselin–Reiss hypothesis) (Ghiseling 1974; Reiss 1989), (2) where population densities are low, receptive females are scattered thus being a limited resource, so selection favors strategies that confer competitive advantages and anti-predatory behavior in the male spiders, (3) females impose direct selection by sexual cannibalism, which posits that small males have an advantage of escape against possible attack by the female during or after mating, or the male would not be attacked because due to its size because it is too small to be considered as prey (Elgar and Fahey 1996); and (4) the sexual maturation hypothesis, that males which reach sexual maturity early (i.e., smaller sizes), have a greater chance to mate before they die (Vollrath and Parker 1992).

Extreme sexual SSD is usually observed in those species that inhabit vertical substrates and the female exceeds a certain size (Moya-Laraño et al. 2009). This is mainly due to the sexual selection pressures that would favor those males that climb branches and access females more quickly in terms of locomotion (Moya-Laraño et al. 2002, 2009). This is known as the gravity hypothesis (GH), which develops the idea that smaller animals climb faster due to their low mass (Moya-Laraño et al. 2002, 2009) Although empirical evidence is lacking to support the existence of selection pressures against the size of males (Foellmer and Fairbairn 2005; Kasumovic et al. 2007; Prenter et al. 2010a), thanks to the model proposed by Moya-Laraño et al. (2002, 2009) the GH has been more widely accepted than others. This model indicates that the rate of climb is inversely proportional to size, at least in spiders in which female body length is >7.6 mm (Foellmer and Moya-Larraño 2007), and that live in high patches within the foliage (Moya-Laraño et al. 2009). Ramos et al. (2004) demonstrated that size sexual dimorphism in a spider of the genus *Theridiidae*, in which the adult male is 1 % of the size of the female, could even result in an evolutionary conflict, since the male has two structures evolved for reproductive activities corresponding to 10 % of the total body size. These structures interfere significantly in its movement performance, which the male solves by removing voluntarily one of these structures, increasing maximum speed by 44 %, resistance by 63 % and distance traveled by 300 % (Ramos et al. 2004). In this case, the characteristics of this species of spider are consistent with the requirements of the model of Moya-Laraño et al. (2009) for extreme size sexual dimorphisms. Also, in a latter paper Corcobado et al. (2010) improved the GH proposing that bridging locomotion (i.e., walking upside-down under self-made silk bridges) may be behind the evolution of extreme SSD. Physical constraints make bridging inefficient for large spiders. Thus in species where bridging is a very common mode of locomotion, small males, by being more efficient at bridging, will be competitively superior and enjoy more mating opportunities. This "Bridging

GH" provides good insight for the controversial question of what keeps males small and also contributes to explain the wide range of SSD in spiders.

However, Brandt and Andrade (2007a, b) using the spider genus *Latrodectus* (which meets the requirements of the GH) questioned the allometric principles used by Moya-Laraño et al. (2002), concluding theoretically and empirically that climbing speed should be independent of size (Brandt hypothesis: BH). Moreover many cursorial spiders also have strong sexual dimorphism although this may be explained by selection for larger female size; it could also be explained by selection of a small male size.

With this background the following question is valid: is climbing velocity the only trait under selection pressure that can produce reduction in the size of males? The aim of this paper is to review the role of energy in SSD of spiders, even for those spiders that do not necessarily live in high foliage, using physical and allometric principles.

2 Analyses

2.1 GH–BH Controversy

To understand this controversy we reviewed the allometric basis of the development of the gravitational hypothesis, which indicates that the effect of gravity on an animal that rises vertically can be described by the physical concept of power (P), energy (E), time (t) and potential energy (E_p, Hecht 1997).

$$P = E/t \tag{1}$$

To climb vertically a given height (h), the work done by the animal must compensate for the difference in potential energy

$$Ep = mgh, \tag{2}$$

where m is the mass, g is the acceleration of gravity, h is the height climbed and t is time.

$$P = mgh/t \tag{3}$$

Replacing h/t by speed (v) and rearranging:

$$v = P/mg \tag{4}$$

Moya-Laraño et al. (2002) based their theoretical development of the GH on McMahon (1983), who stated that the power generated by an animal is proportional to the cross-sectional area of the muscle. As for isometric growth, this section is proportional to the square of the length (L), thus we have

$$P \propto L^2, \tag{5}$$

and since the mass is proportional to L^3, then:

$$v \propto L^2/L^3 g, \text{ or } v \propto L^{-1}. \tag{6}$$

Thus Moya-Laraño et al. (2002) concluded that the speed achieved by an animal that climbs is inversely proportional to its size, so that with females that climb, selection pressures would favor small males that reach the female faster than those of larger males (during mating competition as sexual selection or to avoid predators as natural selection).

However, Brandt and Andrade (2007a) predicted different results than the GH. They argued that the total mechanical force exerted by a muscle is proportional to its cross-sectional area, because total force is the product of the force of a single fiber multiplied by the number of fibers and the number of muscle fibers comprising a muscle is proportional to its cross-sectional area (Alexander 2003), thus

$$F \propto L^2. \tag{7}$$

Although this proposition aroused some criticism (see Brandt and Andrade 2007b) because muscles can activate a variable percentage of their fibers, and muscles are engines that have a working cycle during which they transform chemical energy into mechanical energy, being the power output and not muscle force the biomechanical property that drives locomotion. Brandt and Andrade (2007b) argued that the assumption that power output limits climbing speed, an assumption shared by the GH and BH models, implies maximum muscle performance which requires activation of all muscle fibers, thus the scaling of maximum force to muscle cross-sectional area arises from the parallel arrangement of muscle fibers and the serial arrangement of sarcomeres. This also agrees with the fact that the force produced per muscle cross section has been shown to be constant across a wide range of body sizes and animal taxa (McMahon 1983; Medler 2002).

Following the reasoning of Brandt and Andrade (2007a), since power is defined as the force generated over a distance "x" which is proportional to the length ($x \propto L$), per unit time, then:

$$P = Fx/t, \ \ P \propto L^2 L/t \tag{8}$$

Therefore, ignoring the (1/t) term, Brandt and Andrade (2007a) proposed that:

$$P \propto L^3 \propto m$$

And as the climbing speed is $v = P/mg$, then $v = m/mg = 1/g$ would be a constant; therefore Brandt and Andrade (2007a) suggested that the rate of climb is independent of size, which was empirically showed in a climbing spider (*Latrodectus hesperus*); they suggested that this species does not satisfy the GH. However this proposition has two points of criticism: the already mentioned relationship between force and muscle cross sectional area and ignoring the term (1/t).

The power output $P = Fx/t$, and thus $P = mgv$ and $v \propto P/L^3 g = F(L/t)/L^3 g = F/L^2 tg$. Dimensionally

$$F = ma \propto L^3 L/t^2 = L^4/t^2 \tag{9}$$

and then

$$v \propto L^2/t^3 g \tag{10}$$

and according to the principle of biological similarities (Lambert and Teissier 1927; Günther and Morgado 1996, 2003): $t \propto M^{1/3}$ or $t \propto L$. Thus, again $F \propto L^2$ (from 9) and $v \propto L^{-1}$ (from 10) obtaining the same result as Moya-Laraño et al. 2002, agreeing that power output scales with L^2 (from 8) and also that the force exerted by a muscle varies in direct proportion to its cross-sectional area (McMahon 1983; Medler 2002; Alexander 2003; Biewener 2003; Brandt and Andrade 2007a, b). Thus we propose that the center of the controversy is not whether the force scales with L^2 because there are several reasons to think that this is correct, but rather ignoring the term (1/t) in the analyses.

Thus an inverse relationship between speed and body size would be expected. However, Foellmer and Moya-Laraño (2007) reported that using a large body-mass range of spiders of different instars (0.2–881.4 mg) and phylogenetic affiliation they found that the empirical relationship between body size and climbing speed is not purely negative but curvilinear, with an optimal body size for climbing at approximately 42.5 mg (approximately 7.6 mm), above which the negative relationship predicted by the GH arises. This may indicate that other principles are implicated in the determination of the morphology of spiders and climbing speed.

2.2 Looking for Other Locomotion Principles

According to the principle of dynamic similarity (Alexander 2003), if gravity is important two motions are dynamically similar only if they have equal values of the Froude number (v^2/gL) and as a consequence time would be proportional to the square root of the length: $t \propto L^{0.5}$, giving $v \propto L^{-0.5}$ (using 10).

Here the speed of climbing itself would be inversely proportional to size, but with an allometric exponent of lower magnitude than that proposed in the GH ($-0.5 \neq -1$).

If we consider that spiders also walk horizontally, according to the geometric similarity and dynamic similarity principles for cursorial locomotion, speed can be calculated as stride frequency (f) times stride length (L_z):

$$v = fL_z$$

where the frequency is inversely proportional to the square root of the length (Alexander 2003) and the stride length is proportional to the length:

$$v = L^{-0.5}L^1$$

$$v = L^{-0.5}L^1 \propto L^{0.5} = \sqrt{L}. \tag{11}$$

In this case velocity increases with size, which is qualitatively different from the previous proposals. However, this is not a mistake, since the climbing speed was calculated through energy principles (Moya-Laraño et al. 2002; Brandt and Andrade 2007a, b) and the horizontal velocity was calculated according to inertial limb length principles using the pendulum model (Alexander 2003). Thus if the speed of the male is important for reproduction and is subject to positive selection for horizontal movements, male spiders are expected to be long-legged. Also Moya-Laraño et al. (2008) showed that spiders have evolved following the expectations of pendulum mechanics. First, spiders that move suspending their bodies have evolved disproportionately longer legs relative to wandering spiders. Second, in a species of suspensory spiders they showed that longer legs allow faster suspensory movement and that these spiders are much faster as pendulums than as inverted pendulums. They also showed a positive linear relationship between log speed and log tibia length in both spiders bridging underneath a silk line (i.e., pendular motion) and running on the ground (i.e., inverted pendular motion) forces.

Thus the speed of cursorial and climbing spiders is not only governed by potential energy principles but also by pendulum dynamic similitude, which might explain the curvilinear relationship between speed and length.

2.3 Looking for Other Characters under Selection: Low Energy Expenditure and Low Cost of Transportation

It is also possible that the main target of selection is not the speed of the spider, but another trait related to locomotion performance such as the power of movement and cost of transport.

Total energy expenditure during locomotion is the result of all basal metabolic functions, internal kinetic energy due to muscle movement and the work to translate the body mass. If we take the expended energy of a body during locomotion as the maximum exercise-induced metabolic rate, we see that an allometric exponent of 0.86 ($L^{2.58}$) has been found for insects during flight (Niven and Schaarlemann 2005) and 0.856 ($L^{2.57}$) for typical arthropods (non-ticks, non-scorpions) at 25 °C (Lighton et al. 2001). Also in mammals according to White and Seymour (2005) maximum metabolic rate scales with body mass with an allometric exponent of 0.87 (or $L^{2.61}$), i.e., selection pressures for minimum energy expenditure act in the direction of small body sizes. Through previous dimensional analysis but taking into account the Euclidean time scale, used for macroscopic phenomena and physiological functions that have been found associated with phenomena such as conduction velocity in nerve fibers, velocity in the aorta and vena cava and airflow in the trachea (Günther and Morgado 1996), power (P) can be described as $P \propto L^2$ which is not very similar to that described for maximum exercise metabolism in insects or other arthropods ($P = L^{2.57-2.58}$). However, considering that maximum metabolic rate includes not only mechanical work but also intrinsic work with time-averaged variables of a constant locomotion speed (average acceleration is zero) and other metabolic costs, if we perform the same dimensional analysis but with the fractal criterion of time scale which is used in turnover phenomena that involve a set of microscopic physiological phenomena, intra-organism or cellular level diffusion, respiratory

cycles, cardiac cycles, circulation time, oxygen consumption and water turnover (Günther and Morgado 1996), where $T = M^{1/4} = L^{3/4}$, we obtain

$$P = L^5/T^3 = L^5/L^{9/4} = L^{11/4} = L^{2.75}. \tag{12}$$

Although the applicability of a fractal network model to the scaling of metabolic rate in arthropods (insects) has been questioned (Chown et al. 2007), alternative cell size models suggesting that the scaling of metabolic rate is a by-product of the way in which body size changes, by cell size or number, or some combination of these, yields the same allometric exponent for metabolic rate at interspecific level. Also, a range of allometric exponents that includes the value expected by the fractal model at the intraspecific level was proposed. In the case of why male spiders have reduced their size (intraspecific change) the cell size model could be important, but this not changes significantly the advanced allometric exponent. Thus the relationship derived here (12) is more realistic and very close to the empirical allometric exponent of exercise-induced maximum metabolic rate for arthropods and also for mammals ($P = L^{2.57-2.58}$).

Similarly, empirical evidence shows that mass-specific costs of transport (CoT/M) and velocity (v) for both vertebrates and invertebrates are related to mass through

$$CoT/M = aM^{-0.32} + (bM^{-0.3}/v) \text{ (Taylor et al. 1982)}$$

Factoring and approximating using $M^{-0.02} = 1$

$$CoT/M = M^{-0.3}(a + b/v) \text{ or } CoT \propto L^3 xL^{(3x-0.3)}(a + b/v) = L^3 xL^{-0.9}(a + b/v)$$
$$= L^{2.1}(a + b/v); \text{ for high speed } CoT \alpha L^{2.1}.$$

Now, if we analyze CoT using dimensional analysis, we have that $CoT = E/L = MaL/L = L^3 (L/T^2) L/L = L^4/T^2$. By Lambert and Teissier (1927), $CoT = L^4/L^2 = L^2$. This is coincident with the empirical $CoT = L^{2.1}$. Lambert and Teissier (1927) applied this here because it represents macroscopic displacement.

These analyses tell us that maximum energy expenditure increases with $L^{2.57-2.58}$ and that costs of transport (CoT) of animals walking or running on the ground increase almost proportionally to the square of the length ($CoT \propto L^{2.1}$) and both are interpreted in this study as being variables as important as climbing speed, taking into account that there is no tradeoff between climbing speed and locomotion speed on a horizontal surface (Prenter et al. 2010b).

3 Discussion

The problem of SSD in spiders has not been resolved. The fecundity advantage hypothesis is based on the correlation between female body size and fecundity and it is sufficiently established to explain the big size of a female (Head 1995). Hormiga et al. (1995) showed that in Tetragnathidae family, the body size of males of the

genus *Nephila* decreases with respect to its hypothetical ancestors and close relatives, but females were significantly larger. Thus in this case SSD is not a case of male dwarfism but female gigantism. However in a larger phylogenetic study the same authors showed a more complex panorama in which females increase body size in some genera while the males decrease and females increase body size in others (Hormiga et al. 2000). The sexual maturation hypothesis (Vollrath and Parker 1992) also has been questioned because when the probability of death before reproductive age is high, for example due to predation, natural selection favors early maturation with smaller adult size (Stearns 1992). But for example in the *Nephila* species the probability of male survival is after the reproductive age and thus a possible evolutionary response to predation pressure of adults would be a larger body size (Santos 2007). Another premise of the sexual maturation hypothesis and also of the Ghiselin Reiss hypothesis is that differential mortality of males leads to decreased competition between males for females. However in webs of *Nephila* species usually several males (up to 8) with intense competition for the female has been observed (Robinson and Robinson 1976; Christenson and Goist 1979; Elgar and Fahey 1996). The cannibalism hypothesis is now controversial with studies that agree (Elgar et al. 2000) and others that do not agree with this hypothesis (Uhl and Vollrath 1998). However from this point of view two opposite forces would operate on male size, one of intra-sex competition leading to larger males and the other of avoidance of female aggressive behavior leading to smaller males. The result of these processes would be a stabilizing selection of the male size (Santos 2007).

Another hypothesis related to early maturation and SSD is the sperm precedence reported in spiders. This would lead to an early maturation of males (protandry) and in consequence to small body size of males (LeGrand and Morse 2000), however sperm precedence is present in spiders with high and low SSD and also species that present protandry may have males of large body size (Jackson 1986; Gunnarson and Jhonson 1990). In any event sperm precedence imposes a pressure for a first and speedy mating by the male (Christenson 1989; Elgar 1998).

The GH also has several problems, for example *L. hesperus* does not fit this hypothesis (Brandt and Andrade 2007a, b) and also the analyses of Foellmer and Moya-Larraño (2007) found a curvilinear relationship between body size and speed over several species of spiders, showing that the principles underlying this relationship are not simple and not only related to power output. Both results with *L. herperus* (Brandt and Andrade 2007a) and the curvilinear relationship (Foellmer and Moya-Larraño 2007) would suggest other factors intervening in determine the speed of spiders, for example the type of substrate in which the spiders walk and the limb length. It is interesting that in the results of Brandt and Andrade the repeatability of climbing speed experiments was low and that the sign of the correlation between body mass and speed, although no significant, was inverted when more species were included in the analyses. This may be consistent with a lack of sufficient variation in size of the spiders in *L. hesperus*, but also in the results of Foellmer and Moya-Larraño (2007) the relationship between body mass and speed over a larger number of species, different instars and body masses was negative only over 7.6 mm (approximately 42.5 mg) suggesting that bellow this threshold other principles may be operating. For example body size is positively
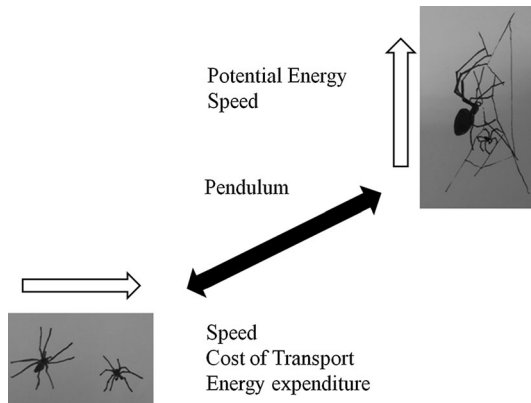
Fig. 1 Main physical principles accounting for sexual SSD. *White arrows* represent horizontal and vertical displacement. Potential energy is relevant in vertical movements and in determining the climbing and bridging speed favoring male small size. Energy expenditure and cost of transport are relevant in horizontal displacements favoring small male size. Pendulum mechanics is relevant in both horizontal and vertical movements favoring long legs

correlated with limb length and horizontal speed (Garland and Losos 1994; Alexander 2003), thus long legs, as pendulum model predicts, may be the factor that explains these results.

We propose that the cost of transport or equivalently the energy expenditure is also a trait under selection pressure in male spiders (not only climbing speed), favoring those of smaller size to reduce travel costs. This fit with the Ghiselin–Reiss hypothesis (G–RH) which states that probability of males congregating around receptive females is low that male–male competition is relaxed, thus conferring advantage to smaller males. Al so states that smaller males have an advantage because their relatively lower energy demand allows these males to be able to devote more time to mate searching. This would be most relevant when male–male competition is not too high or when female density is low (Foellmer and Moya-Larraño 2007) in cursorial spiders.

Additionally, increased limb length may increase motor performance in several animals (Grossi and Canals 2010), and also in spiders, in which locomotion would be governed by the interaction of inertial and gravitational forces as predicted by the pendulum model (Corcobado et al. 2010).

In the particular case of the climbing spiders, low transportation costs, low energy expenditure and high climbing speed would be favored by a small body size. But in the more general case, we propose that G–RH applying in wandering spiders and GH applying in climbing and bridging spiders are two extremes of a more general principle of minimum energy expenditure and CoT to explain sexual SSD, that not only applies to climbing spiders, but also includes those that are cursorial and environmentally not associated with arboreal life, since climbing speed would not be the only variable under selection pressure, but energy expenditure and costs of transport as well, which would account for this phenotypic difference between the sexes.

If so, we propose that there are several energetic forces favoring sexual SSD, when males are sexually mature. In this situation the male is responsible for tracking the female, thus moving relatively more than she does, even in periods of prolonged fasting (Foelix 1996; Aisenberg et al. 2007). In this period the costs of locomotion would impose higher selection pressures for low cost of transport, low energy expenditure or high speed. The morphology of spiders responds to these selective forces depending upon the lifestyle of the spiders (Fig. 1). Climbing and bridging spiders must overcome the force of gravity. If bridging allows faster dispersal, small males would have a selective advantage by enjoying more mating opportunities. In wandering spiders with low population density and in consequence low male–male interactions, high speed and low power output or cost of transport should be favored by natural selection. Pendulum mechanics show the advantages of long legs in spiders and their relationship with high speed, even in climbing and bridging spiders (see Moya-Laraño et al. 2008). So a small size, compensated with long legs should be the expected morphology of a fast and mobile male spider.

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