Consequences of sexual size dimorphism on energetics and locomotor performance of *Grammostola rosea* (Araneae; Teraphosidae)

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Abstract. Most male spiders are smaller than females; during sexual maturity, males change their behaviour, abandoning their web or nest to seek out receptive females actively, whereas females stalk prey near their web or nest and tend not to move away from it. Considering this behavioural difference to be associated with increased locomotor activity at maturity, it may be hypothesized that males will have traits that increase locomotor performance. The present study examines the kinetics and energetics of the movements of the mygalomorph spider *Grammostola rosea* Walckenaer, a large spider with sexual size dimorphism. It is found that males have a higher maximum aerobic speed, average speed, distance travelled and critical angle of climbing than females, indicating better performance. Males also have lower costs of transport than females. These results support the hypothesis that sexual dimorphism in wandering spiders with active males, which are characterized by smaller body size and longer legs than the larger and more static females, is associated with low transport cost, high velocity and better locomotor performance.

Key words. Locomotion, performance, sexual dimorphism, spiders.

Introduction

In some animal species, the males have a larger body size than females. This pattern may be related to an increased reproductive success in males with large body size in intrasexual competition for females or the result of an increased probability to be chosen by the female (Darwin, 1871; Andersson, 1994; Fairbairn, 1997; Eberhard, 2000). In many invertebrate and some vertebrate animals, the sexual size dimorphism is characterized by females being larger than males (Zamudio, 1998; Blanckenhorn, 2005; Kruger, 2005). This is the case for several spiders in which extreme examples of sexual size dimorphism are found (Grossi & Canals, 2015). The origin of the sexual size dimorphism is still controversial and depends on each particular taxonomic group

in which such dimorphism is found. This could be explained by natural or sexual selection for large female size or small male size, or both (Ghiselin, 1974; Reiss, 1989; Vollrath & Parker, 1992; Head, 1995; Elgar & Fahey, 1996; Eberhard, 2000; Kruger, 2005; Foellmer & Moya-Larraño, 2007; Santos, 2007; Sánchez-Quiróz *et al.*, 2012).

Sexual size dimorphism may originate as a result of different combinations of factors and selective pressures. First, this may be solely result from an increase in the size of the female; for example, as a consequence of a correlation between body size and clutch size as postulated by the fecundity hypothesis (Head, 1995; Prenter *et al.*, 1999). Second, sexual size dimorphism may result from a reduction of male size, as postulated by several hypotheses: (i) where population densities are low, there is relaxing of selection for large male size (Ghiselin, 1974; Reiss, 1989); (ii) where population densities are low, selection favours strategies that confer competitive advantages and anti-predatory behaviour in the male spiders (Ghiselin, 1974; Reiss, 1989); (iii) females may impose direct selection

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by sexual cannibalism, which is avoided by small males (Elgar & Fahey, 1996); (iv) in the sexual maturation hypothesis, males that reach sexual maturity early (i.e. smaller sizes) have a greater chance to mate before they die (Vollrath & Parker, 1992); and (v) small males have lower energetic and locomotion costs than females (Moya-Laraño *et al.*, 2002, 2009; Grossi & Canals, 2015). Furthermore, sexual size dimorphism may result from both an increase in female size and a decrease in male size (Hormiga *et al.*, 2000) and from an increase or decrease of size in both sexes but at different rates (Hormiga *et al.*, 2000). In a phylogenetic analysis of 80 genera of spiders, Hormiga *et al.* (2000) show that the monomorphic trait in spiders is a primitive condition and that sexual dimorphism is a derived character, which, in some cases, has been inverted on more than five occasions in one family (Aranae, Argiopidae).

Extreme sexual size dimorphism is usually observed in those species that inhabit vertical substrates and in which the females exceed a certain size (Moya-Laraño *et al.*, 2009). This is mainly a result of the sexual selection pressures favouring those males that are able to climb branches and can access females more quickly (Moya-Laraño *et al.*, 2002, 2009). This is known as the gravity hypothesis, which develops from the idea that smaller animals climb faster as a result of their low mass (Moya-Laraño *et al.*, 2002, 2009), although empirical evidence is lacking to support the existence of selection pressures against male size (Prenter *et al.*, 1999, 2010; Foellmer & Fairbairn, 2005; Kasumovic *et al.*, 2007). Grossi & Canals (2015), using physical and allometric principles, review the role of energy in sexual size dimorphism of spiders even for those spiders that do not necessarily live in high foliage, interpreting this type of sexual size dimorphism as an example of a low energetic cost design.

Most male spiders have smaller body masses than females; during sexual maturity, males change their behaviour, abandoning their web or nest to seek out receptive females actively, whereas females stalk prey near their web or nest and tend not to move away from it (Shillington & Peterson, 2002; Foelix, 2011). Considering that this behavioural difference is associated with increased locomotor activity at maturity, it may be expected that males have traits increasing locomotor performance. On the basis of a theoretical analysis of the speed, energetics and costs of transport, and the allometric relationships of these variables with body mass, Grossi & Canals (2015) propose that small body size combined with long legs is energetically beneficial for wandering spiders, increasing their locomotor efficiency. Thus, adult males may be expected to have longer legs than females as consequence of positive allometry (observed exponent higher than that expected by dimensional analysis) (Grossi *et al.*, 2016). Long legs are related to high speed in spiders that walk on the ground, which may be a determinant in opportunities to copulate.

There is evidence for sexual dimorphism in the leg lengths of ground-living spiders (Gasnier *et al.*, 2002; Framenau, 2005). This idea is supported by studies on the locomotory activity of wolf spiders, in which males are the more active sex (Framenau *et al.*, 1996; Framenau, 2005); for a counter example, see Aisenberg *et al.* (2010). Data on leg length in wolf spiders show comparatively longer legs for males than females, although only after the final moult, suggesting its significance in reproductive

behaviour, such as searching for mates (Framenau, 2005). Sexual dimorphism is also been reported in spiders of the family Mygalomorphae. As in wolf spiders, adult males of the mygalomorph spiders have longer legs than females (Calderon *et al.*, 1990; Costa & Pérez-Miles, 2002; Santos, 2007; Grossi *et al.*, 2016).

In wandering spiders with low population density, and as a consequence of this few male–male interactions, high speed and low energy expenditure or the cost of transport should be favoured by natural selection. Pendulum mechanics show the advantages of long legs in spiders and their relationship to high speed, even in climbing and bridging spiders (Moya-Laraño *et al.*, 2008. Small size is related to a low cost of transport. Thus, a small size that is compensated by long legs should be the expected morphology for a fast and mobile male spider (Grossi & Canals, 2015).

Sexual differences in behaviour and several life-history characteristics are also associated with sexual size dimorphism (Ghiselin, 1974; Vollrath & Parker, 1992; Elgar & Fahey, 1996; Hormiga *et al.*, 1995, 2000). When spiders reach sexual maturity, the males locate the females and reproductive events occur (Shillington & Peterson, 2002; Stoltey & Shillington, 2009; Foelix, 2011). The energetic budget associated with these different sexual behaviours could be the origin of differences in traits such as metabolic rates and physiological performance (Shillington, 2005).

In the present study, it is proposed that body size and leg length could be under selective pressures mediated by locomotor performance expressed through maximum aerobic speed (VA_{max}) and the minimum cost of transport (CoT_{min}) (Grossi & Canals, 2015; Grossi *et al.*, 2016). Thus, as associated with sexual size dimorphism, it is expected that, in those species of spider in which the males are smaller, males will have a better ambulatory efficiency, a higher speed and a better climbing performance compared with their larger conspecific females.

Materials and methods

Animal model

Grammostola rosea Walckenaer is a large wandering mygalomorph spider showing sexual size dimorphism (Grossi *et al.*, 2016). It inhabits mainly arid and semi-arid regions in the lowlands near mountain environments of sclerophyllous forest and Mediterranean scrubland in Northern Chile (i.e. habitats characterized by cold, wet winters and hot, dry summers). It may be found in areas of low vegetation or in specific areas of slopes or soft ground, where it builds burrows up to a depth of 45 cm (Canals *et al.*, 2008; Alfaro *et al.*, 2013).

Fifty individuals of *G. rosea*, 25 females [body mass $(M_b) = 16.71 \pm 2.37$ g; mean $\pm$ SD] and 25 males $(M_b = 10.10 \pm 1.19$ g), were captured in Colina, north of Santiago, Chile (33°11′S, 70°40′W). The individuals were taken to the laboratory and kept in individual terraria (24 cm × 12 cm × 10 cm) at 25 °C under a LD 12:12 h photocycle, with water available *ad libitum*. The spiders were fed weekly with five larvae of *Tenebrio molitor* to maintain the

body weight at capture, based on the estimations of Canals *et al.* (2012). Each spider was immobilized via a dorsoventral compression elastic device applied to the prosoma of the spider. Each spider and a reference mark of 50 mm were photographed with a D70 camera (Nikon, Japan). The image file was analyzed with the morphometric software IMAGEJ, version 1.47b (https://imagej.nih.gov/ij) to measure the body length.

Respirometry and velocity

A flow-through respirometry system (FOXBOX; Sable Systems International, North Las Vegas, Nevada) was used for metabolic measurements, in accordance with the respirometry protocol for arthropods (Lighton *et al.*, 2001; Shillington & Peterson, 2002; Nespolo *et al.*, 2011). Gaseous CO_2 release was measured in a continuous flux system ($520 \, mL \, min^{-1}$), after previously removing CO_2 and water with barium hydroxide and calcium sulphate, respectively. Individuals were introduced into a cabinet of $10 \, cm \times 15 \, cm \times 4 \, cm$ ($600 \, mL$) that contained a treadmill of 15 cm, which was connected by means of a sealed bearing to an external DC motor. This cabinet was inside a light and temperature-controlled chamber at $30 \, °C$ that had a digital camera connected to a computer for monitoring spider behaviour. Data were STP (standard conditions of pressure and temperature) corrected and analyzed using EXPEDATA, version 1.0.3 (Sable Systems International). Each specimen was placed on the treadmill in the cabinet. First, metabolic rate (CO_2 release: resting metabolic rate; RMR) with a treadmill speed $V_0 = 0 \, m \, h^{-1}$ at $30 \, °C$ was measured for 45 min at midday, which corresponds to the inactivity period of this species. Then metabolic rates at V_1 ($25 \, m \, h^{-1}$), V_2 ($50.4 \, m \, h^{-1}$), V_3 ($72.0 \, m \, h^{-1}$) and V_4 ($122.4 \, m \, h^{-1}$) were recorded for 8 min each. These treadmill velocities were selected by considering one velocity in which anaerobic metabolism was expected (V_4), based on Shillington & Peterson (2002) and three almost equidistant points below this value. Only the last 3 min of exercise on the treadmill were used for the analyses, when the pattern of CO_2 release was stabilized. Spiders with erratic behaviour were not used for the metabolic analyses.

To estimate CoT_{min}, which is the minimum energy expenditure per distance travelled, a regression line between metabolic rate against speed was estimated using V_1, V_2 and V_3, excluding V_0 because RMR is lower than the intercept of this line, which represents the cost of position (P_c) (Herreid *et al.*, 1981). Also, V_4 was excluded because, at this speed, there is anaerobic metabolism (MR_{v4}) in spider physiology (Shillington & Peterson, 2002). With these considerations, the slope of the regression line represents the CoT_{min} (Schmidt-Nielsen, 1972; Hoyt & Taylor, 1981; Herreid & Full, 1984; Shillington & Peterson, 2002). The speed at which this line and V_4 intersect corresponds to the maximum aerobic speed (VA_{max}).

Ambulation experiments

The same 50 individuals of *G. rosea* were introduced individually into a circular experimental arena (diameter 1.2 m) with smooth walls (height 75 cm). The mean $\pm$ SD body lengths of the spiders were $4.25 \pm 0.22 \, cm$ in males and $5.05 \pm 0.30 \, cm$ in females, which represent between 3.5% and 4.2% of the arena diameter, allowing free movement of animals. The entire experimental arena was cleaned after each experimental trial, removing chemical cues. In each trial, the spiders were placed in the centre of the arena and were left to roam freely. The ambulation was recorded with a DCR-SX40 digital camera (Sony, Japan) for 1 h at a constant temperature of $30 \, °C$. The videos were analyzed with the video tracking software ETHOVISION XT (Noldus Information Technology Inc., Leesburg, Virginia), measuring the variables: distance (d), the total activity time (A_t) and the speed in the sample interval of 1 s (3600 samples in 1 h). With these measured variables, the maximum speed (v_{max}) and average speed (v_{mean}) were estimated.

The same individuals of *G. rosea* were placed individually in the centre of a folding smooth rectangular particleboard of $50 \times 20 \, cm$ with a smooth surface, attached to a hinge carrying a goniometer. The board was initially horizontal then the tilt angle was varied at a rate of $6° \, seg^{-1}$ until the spider slipped. This angle was measured using five replicates for each individual and the average of these replicates was computed and was called the critical tilt angle of climbing (α_c).

Statistical analysis

All statistical analyses were performed with STATA, version 11.0 (StataCorp LP, College Station, Texas). The significance level was $\alpha = 0.05$. For all analyses, assumptions of normality and homoscedasticity were checked with the Kolmogorov–Smirnov and Levene's tests, respectively.

Metabolic rates (response variable) at all speeds were first compared with a repeated measures analysis of variance, considering sex and speed (repeated measure) as independent variables. Multiple comparisons were performed using Tukey's test. Then the relationship between metabolic rate and speed ($V_1 - V_3$) was studied with linear regression analysis, determining the slope that represents CoT_{min}. A covariance analysis for homogeneity of slopes was used to compare the curves of both sexes. RMR and MR_{v4} between sexes, which were not used in the regressions, were compared with Student's *t*-test. The VA_{max} between sexes and RMR and P_c in each sex were compared with Student's *t*-tests.

Student's *t*-tests were used to compare d, A_t, v_{mean}, v_{max} and α_c between sexes. For each sex, a regression analysis was performed between each variable on body mass. To satisfy the assumptions of normality and homoscedasticity, the variables were log transformed. Finally, both sexes were pooled and a new regression analysis was performed.

Results

Energetics

As expected, there were differences in metabolic rates at different speeds in males and in females tested separately

Table 1. Absolute (VCO_2) and mass-specific (VCO_2/M_b) CO_2 release of *Grammostola rosea* at different walking speeds at 30 °C.

Velocity (m h^{-1})	Females (16.7 ± 2.4 g)		Males (10.1 ± 1.2 g)	
	VCO_2 (μL h^{-1})	VCO_2/M_b (μL g^{-1} h^{-1})	VCO_2 (μL h^{-1})	VCO_2/M_b (μL g^{-1} h^{-1})
0[a]	353.6 ± 99.8	21.69 ± 6.12	243.48 ± 76.17	24.59 ± 8.53
25[b]	1058.2 ± 285.6	63.28 ± 14.3	953.5 ± 277.6	94.75 ± 25.35
50.4[c]	1558.3 ± 299.4	93.63 ± 15.70	1415.7 ± 373.3	141.88 ± 38.21
72.0[d]	2058.8 ± 327.9	124.30 ± 19.93	1665.0 ± 370.6	167.31 ± 40.69
122.4[e]	2295.5 ± 380.7	138.58 ± 23.05	2048.0 ± 423.4	205.60 ± 45.85

Different letters indicate differences in Tukey's tests at $\alpha < 0.05$. M_b, body mass. Data are the mean ± SD.
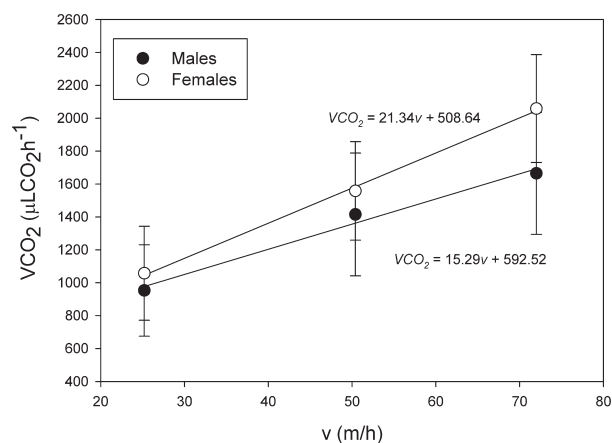

Fig. 1. Gaseous CO_2 release of individuals of *Grammostola rosea* at different walking speeds. The lines represents the regression lines for females ($r^2 = 0.654$; $P < 0.001$) and males ($r^2 = 0.43$; $P < 0.001$), respectively.

(males: $F_{4,120} = 176.71$, $P < 0.001$; females: $F_{4,120} = 112.31$, $P < 0.01$) and also when these were pooled ($F_{4,192} = 777.4$, $P < 0.001$) and all metabolic rates at different velocities were different by Tukey's test (Table 1). Also, the metabolic rate (μL CO_2 h^{-1}) increased with the speed (m h^{-1}) from V_1 to V_3 in males ($r^2 = 0.43$, $F_{1,73} = 54.47$, $P < 0.001$) and females ($r^2 = 0.654$, $F_{1,73} = 135.8$, $P < 0.001$), although the slopes were different (Fig. 1). The CoT_{min} (slopes) in females (21.34 ± 9.15 μL CO_2 m^{-1}) were higher than in males (15.29 ± 10.35 μL CO_2 m^{-1}) ($F_{1,146} = 4.79$, $P = 0.030$) (Figs 1 and 2). This means that females expend almost 40% more energy per distance unit than males. The high slopes determines that females quickly reach the anaerobic metabolism level and that the maximum aerobic speed (VA_{max}) of males (95.20 ± 27.69 m h^{-1}) was higher than that of females (83.74 ± 17.84 m h^{-1}) ($t_{48} = 1.74$, $P = 0.044$) (Fig. 2).

In absolute terms RMR of females (353.56 ± 99.75 μL CO_2 h^{-1}) was higher than that of males and 243.48 ± 76.17 μL CO_2 h^{-1} ($t_{48} = -4.39$, $P < 0.01$), although the mass specific RMR were not different (males: 24.59 ± 8.53 μL CO_2 h^{-1} g^{-1}; females: 21.69 ± 6.12 μL CO_2 h^{-1} g^{-1}) ($t_{48} = 1.35$, $P = 0.18$). Also, the MR_{v4} of females (2295.52 ± 380.67 μL CO_2 h^{-1})

was higher than in males (2048.04 ± 423.39 μL CO_2 h^{-1}) ($t_{48} = -2.17$, $P = 0.034$). In both sexes, the position costs, P_c, were higher than RMR (males: 592.52 μL CO_2 h^{-1} versus 243.48 ± 76.17 μL CO_2 h^{-1}, $t_{24} = 22.91$, $P < 0.001$; females: 508.64 μL CO_2 h^{-1} versus 353.56 ± 99.75 μL CO_2 h^{-1} $t_{24} = 7.67$, $P < 0.01$).

Locomotor performance

The distance d in males (43.35 ± 27.96 m) was larger than in females (25.34 ± 11.97 m) ($t_{27} = -2.23$, $P = 0.03$) and was not correlated with the body mass of the spiders (males: $r^2 = 0.03$, $F_{1,13} = 0.33$, $P = 0.58$; females: $r^2 = 0.002$, $F_{1,12} = 0.03$, $P = 0.86$) (Table 2). However, when males and females were pooled, there was a negative relationship between d and M_b ($r^2 = 0.153$, $F_{1,27} = 4.87$, $P = 0.04$) (Fig. 3), which is explained by the different M_b of males and females because this difference disappears when M_b is used as a covariate ($F_{1,26} = 0.24$, $P = 0.63$).

The A_t was similar in males ($59.02 \pm 24.94\%$) and females ($48.98 \pm 25.90\%$) ($t_{27} = -1.06$, $P = 0.29$) and there was no relationship between A_t and M_b in each sex separately (males: $r^2 = 0.02$, $F_{1,13} = 0.24$, $P = 0.63$; females: $r^2 = 0.06$, $F_{1,12} = 0.75$, $P = 0.40$) or when they were pooled ($r^2 = 0.013$, $F_{1,27} = 0.36$, $P = 0.55$).

The v_{mean} was higher in males ($2.51 \times 10^{-2} \pm 9.4 \times 10^{-3}$ m s^{-1}) than females ($1.9 \times 10^{-2} \pm 6.5 \times 10^{-3}$ m s^{-1}) ($t_{27} = -2.17$, $P = 0.04$) and a negative correlation between v_{mean} and M_b was found in males ($r^2 = 0.376$, $F_{1,13} = 7.838$, $P = 0.01$) and females ($r^2 = 0.298$, $F_{1,12} = 6.52$, $P = 0.02$) separately and also when both sexes were pooled ($r^2 = 0.341$, $F_{1,27} = 13.991$, $P < 0.01$) (Fig. 3). Also, the v_{max} of males ($8.8 \times 10^{-2} \pm 2.3 \times 10^{-2}$ m s^{-1}) was higher than that of females ($6.7 \times 10^{-2} \pm 2.1 \times 10^{-2}$ m s^{-1}) ($t_{22} = -2.40$, $P = 0.03$) and was not correlated with M_b in both sexes separately (males: $r^2 = 0.05$, $F_{1,11} = 0.54$, $P = 0.48$; females: $r^2 = 0.04$, $F_{1,9} = 0.371$, $P = 0.56$) and was only marginally correlated with M_b when both sexes were pooled ($r^2 = 0,119$, $F_{1,22} = 2.991$, $P = 0.098$) (Fig. 3).

The α_c of males (1.47 ± 0.28 radians) was higher than that of females (1.18 ± 0.24 radians) ($t_{30} = -3.15$, $P = 0.003$) and was not correlated with M_b (males: $r^2 = 0.11$, $F_{1,13} = 1.55$, $P = 0.24$; females: $r^2 = 0.0005$, $F_{1,15} = 0.01$, $P = 0.93$).

Discussion

The *G. rosea* spiders show an increase in metabolic rate subsequent to the increment of walking speed in a pattern similar to that described for other arthropods (Herreid *et al.*, 1981; Herreid & Full, 1984; Shillington & Peterson, 2002; Schmitz, 2005; Biancardi *et al.*, 2011). As is proposed in other studies (Herreid *et al.*, 1981), the postural cost (Pc) is higher than RMR in both sexes but, although the females have a higher RMR than the males, the Pc of males is higher than that of females. In the tarantula *Aphonopelma anax* (6.91 g in males and 15.72 g in females), Pc is 2.57 times the RMR in males and 1.81 times the RMR in females (Shillington & Peterson, 2002), which is
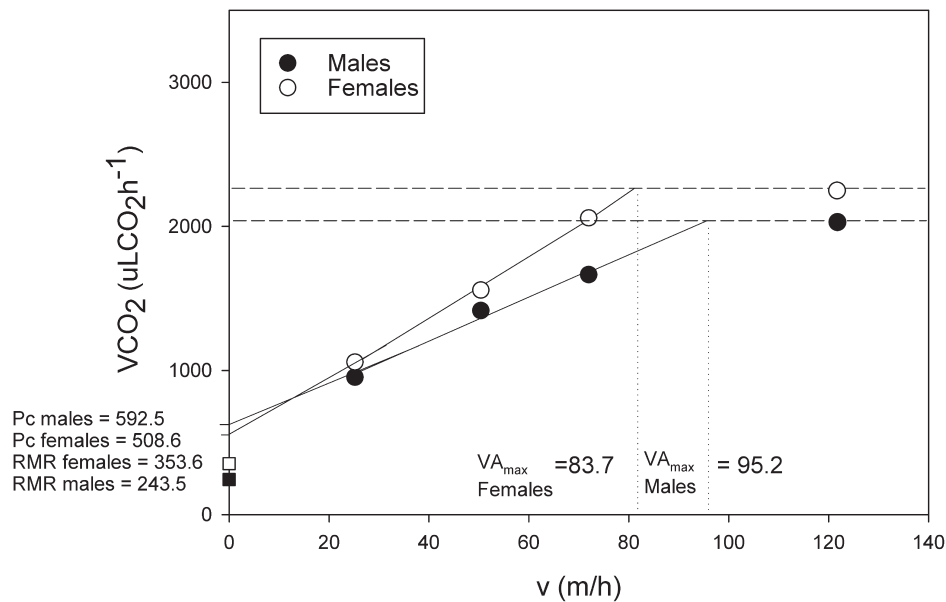
Fig. 2. Maximum aerobic speed (VA_{max}) of individuals of *Grammostola rosea* at different walking speeds. The minimum cost of transport (CoT_{min}), is the slope of the regression line. Intercepts represent the cost of position (P_c), and VCO_2 at $v = 0$ represents the resting metabolic rate (RMR).

Table 2. Ambulation of *Grammostola rosea* during 1 h in a circular experimental arena at 30 °C.

Variable	Females	Males
M_b (g)	17.05 ± 2.52*	10.43 ± 1.15
d (m)	25.34 ± 11.97*	43.35 ± 27.96
A_t (%)	48.98 ± 25.90	59.02 ± 24.94
v_{mean} ($\times 10^{-2}$ m s^{-1})	1.90 ± 0.65*	2.51 ± 0.87
v_{max} ($\times 10^{-2}$ m s^{-1})	6.67 ± 2.06*	8.52 ± 2.43
α_c (°)	67.65 ± 13.54*	84.27 ± 16.28

Distance (d), maximum speed (v_{max}), average speed (v_{mean}) activity time (A_t; percentage of activity times the total time of experimentation) and the critical tilt angle. M_b, body mass. An asterisk (*) indicates a statistical difference at $\alpha < 0.05$. Data are the mean ± SD.

similar to the values found in the present study (i.e. 2.43 for males and 1.43 for females). This sexual difference in P_c may be explained by the long legs of males relative to those of females (Grossi *et al.*, 2016) because long legs involve large bending moments of the joints.

In absolute terms, the RMR of males is less than that of females, as expected from the difference in body mass, although the mass-specific RMR of males is slightly but not significantly higher than that of females, as a result of the great variability in RMR, with coefficients of variation of 35% and 28% in males and females, respectively. However, Shillington (2005) reports that, in the tarantula *A. anax*, with a similar pattern of sexual dimorphism, males of smaller size have a higher absolute RMR than the largest females. Based on a negative correlation between RMR and cost of activity, it is proposed that the increased metabolic rate of males would be an adaptive strategy to sustain the high metabolic demands of locomotor activity when searching for females during the mating season (Shillington,

2005; Stoltey & Shillington, 2009). However, in other studies, the RMR is not reported to be different between sexes or males have lower metabolic rates than females (Humphreys, 1977; Kotiaho, 1998). From an evolutionary point of view, the most parsimonious strategy to reduce the energy budget in an active animal with low food availability appears to be a reduction in body size.

The results reported in the present study show that CoT_{min} in males is lower than that in females, as predicted. Males release 15.289 μL CO_2 per m travelled, whereas females release 21.337 μL CO_2. Also, males show a higher VA_{max} than females, implying increased locomotor efficiency considering that more energy is converted into kinetic energy (higher speed) with the same physiological machinery. These characteristics associated with males having active wandering behaviour may be indicative of an adaptation under selective pressure favouring more efficient males from an energetic point of view. The difference in CoT_{min} between sexes may be explained by the larger body mass of females compared with that of males because the larger the body mass, the greater the transport cost (Grossi & Canals, 2015), with this being valid over a great size range in several organisms (Taylor *et al.*, 1982; Full & Tu, 1991; Biewener, 2003; Langman *et al.*, 2012). In agreement with Shillington & Peterson (2002), the present study finds no inter-sex differences in mass-specific CoT_{min}, suggesting that the metabolic machinery is very similar in both sexes.

Considering that gravity and inertia are relevant in arachnid locomotion in a way similar to that in other animals (Grossi & Canals, 2010), a relationship between the positive allometry of male legs of *G. rosea* (Grossi & Canals, 2015) and their locomotor efficiency can be established. In these animals, velocity is a result of the product of leg length and stride frequency; thus, males with longer legs than females and
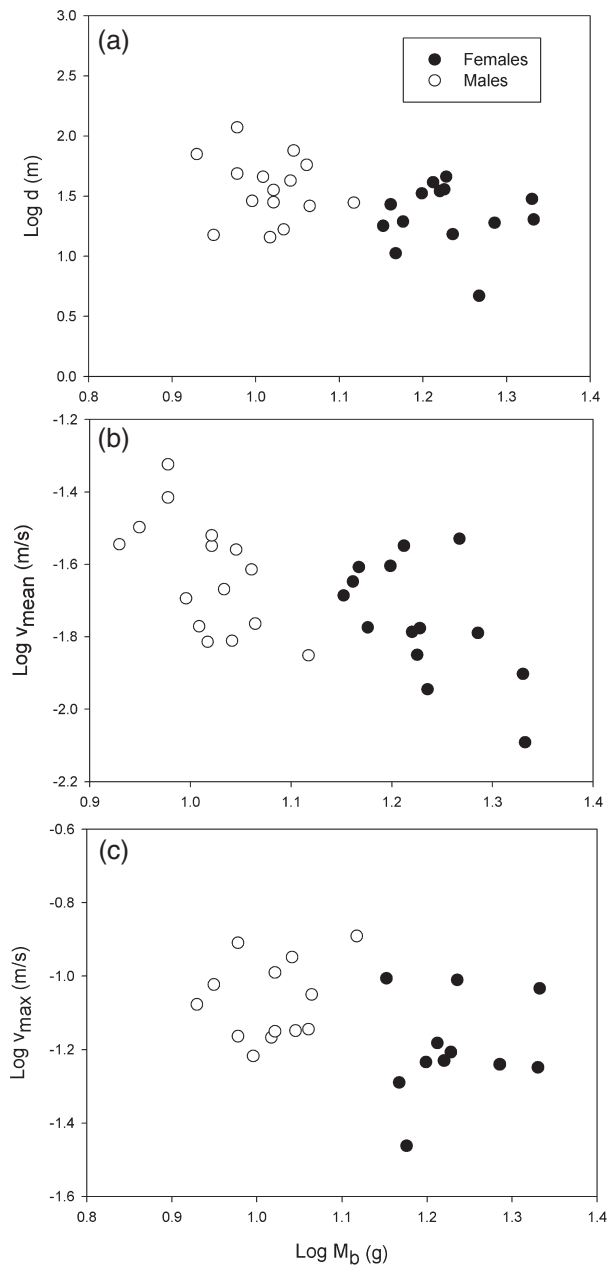
Fig. 3. (a) Log-log relationship between the distance travelled and body mass (M_b) for males and females of *Grammostola rosea*. (b) Log-log relationship between the mean speed and M_b for males and females of *Grammostola rosea*. (c) Log-log relationship between the maximum speed and M_b for males and females of *Grammostola rosea*.

similar movement pattern and stride frequency move faster than females. In this species, the standardized length of the legs of males is approximately 25% longer than that of females (Grossi *et al.*, 2016). Furthermore, in accordance with the dynamic similitude principle (Alexander, 2003), the smaller the body size, the larger the stride frequency, which helps to increase the speed. In the present study, the mean velocity v_{mean} is related to body mass in either sex separately or when the data are pooled,

although v_{max} is only marginally related to body mass. Although the latter variable has been considered to be related to body mass (Moya-Laraño *et al.*, 2002, 2009; Foellmer & Moya-Larraño, 2007; Grossi & Canals, 2015), the results of the present study show that v_{max} is more related to the sex of the individuals, with males reaching higher velocities than females during ambulation, a result consistent with the predictions of the present study and agreeing with the expected negative relationship between velocity and body size. A regression analysis between $\log v_{max}$ on $\log M_b$ shows a nonsignificant regression coefficient of -0.39 ($P = 0.09$). It is interesting to note that, although it is not significant, this could imply a relationship between v_{max} and longitude (L) with an exponent of -1.14 ($= -0.39 \times 3$), which is similar to the exponent of -1 expected between these variables in climbing spiders (Moya-Laraño *et al.*, 2002, 2009) and also in wandering spiders (Grossi & Canals, 2015). However, the recorded velocities correspond to ambulatory velocity in the experimental arena, which may be different from those of male spiders in their natural environment or when they seek females. Males also have a higher v_{mean} and mass-specific v_{mean} than females and also these are negatively correlated with body mass. These and the v_{max} results agree with the results in the treadmill and are probably associated with the long legs of males and the highly efficient intermittent locomotion in male spiders (Krafft & Pasquet, 1991).

In the other ambulation experiments with *G. rosea*, no sexual differences are found in A_t, in agreement with the results reported for other spiders (Stoltey & Shillington, 2009), whereas, despite the high variability, d is significantly longer in males than in females, revealing a high tracking efficiency. This means that smaller males may travel longer distances. Janowski-Bell & Horner (1999) report that the Texas brown tarantula *Aphonopelma hentzi* may travel up to 95 m in 1 day, a result in contrast to that for *G. rosea* in 1 h of experimental trials. Stoltey & Shillington (2009) report that males of *A. anax* (Texas tan tarantula) may travel 90–259 m in a day and do not find a relationship between M_b and distance recorded by telemetry, which appears to be more consistent with the results for *G. rosea*. However, a negative M_b relationship is found for *G. rosea* when the distance travelled by both males and females is included, which can be explained by the large body mass of females. The proportionally longer distance travelled by *G. rosea* may be explained by the experimental conditions of the present study where spiders face an unfamiliar environment, which may increase activities of recognition or escape.

Male *G. rosea* have a higher α_c than females. This result does not agree with results obtained with the white collared tarantula *Eupalaestrus weijenberghi* in which males have lower friction than females on glass, which is interpreted because the intense locomotion of males produces body deterioration and, consequently, wastage of adhesive pads when reducing friction values (Pérez-Miles *et al.*, 2015). Also, no differences are found in α_c among sexes in the eight other species examined, although the number of individuals studied for each species is low. Considering only $\alpha_c < \pi/2$ radians and estimating the friction coefficient by a force diagram (Hecht, 1997), values of 9.96 ± 9.76 are obtained for male *G. rosea* and 2.43 ± 1.88 for

female *G. rosea*. The angle values in the present study are similar to those reported by Pérez-Miles *et al.* (2015) for several Theraphosidae spiders on a glass surface but do not agree with those reported for *Aphonopelma seemanni* (Theraphosidae), with values lower than 1.0 (Niederegger & Gorb, 2006). However, the study by Niederegger & Gorb (2006) uses dead spiders and the friction coefficient is estimated only for isolated metatarsi connected to force transductors. Live spiders may tolerate an α_c greater than 90°, which would imply infinite friction coefficients, although spiders utilize the anisotropic properties of scopula hairs, increasing cohesion with the surface. Thus, the inert surfaces of dead spiders have a lower adherence than the same segments of a live spider (Niederegger & Gorb, 2006; Pérez-Miles *et al.*, 2015).

In summary, the results of the present study support the hypothesis that sexual dimorphism in wandering spiders with active males, which are characterized by smaller body size and longer legs than the larger and more static females, is associated with low transport cost, high velocity and better locomotor performance.

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