

Low metabolic rates in primitive hunters and weaver spiders

MAURICIO CANALS^{1,2}, CLAUDIO VELOSO³, LUCILA MORENO² and RIGOBERTO SOLIS⁴

¹Departamento de Medicina and Programa de Salud Ambiental, Escuela de Salud Pública, Facultad de Medicina, Universidad de Chile, Santiago, Chile, ²Departamento de Zoología, Facultad de Ciencias Naturales y Oceanográficas, Universidad de Concepción, Santiago, Chile, ³Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile, Santiago, Chile and

⁴Departamento de Ciencias Biológicas Animales, Facultad de Ciencias Veterinarias y Pecuarias, Universidad de Chile, Santiago, Chile

Abstract. The rates of oxygen consumption and carbon dioxide release of primitive hunters and weaver spiders, the Chilean Recluse spider *Loxosceles laeta* Nicolet (Araneae: Sicariidae) and the Chilean Tiger spider *Scytodes globula* Nicolet (Araneae: Scytodidae), are analyzed, and their relationship with body mass is studied. The results are compared with the metabolic data available for other spiders. A low metabolic rate is found both for these two species and other primitive hunters and weavers, such as spiders of the families Dysderidae and Plectreuridae. The metabolic rate of this group is lower than in nonprimitive spiders, such as the orb weavers (Araneae: Araneidae). The results reject the proposition of a general relationship for metabolic rate for all land arthropods (related to body mass) and agree with the hypothesis that metabolic rates are affected not only by sex, reproductive and developmental status, but also by ecology and life style, recognizing here, at least in the araneomorph spiders, a group having low metabolism, comprising the primitive hunters and weaver spiders, and another group comprising the higher metabolic rate web building spiders (e.g. orb weavers).

Key words. Haplogynae, metabolism, spiders.

Introduction

Spiders have very low resting metabolic rates (Anderson, 1970; Greenstone & Bennett, 1980; Prestwich, 1983a, 1983b; Wilder, 2011), which may be associated with adaptation to environments of low predictability and low prey availability (Anderson, 1970; Greenstone & Bennett, 1980). Physiologically, this could be the result of spiders using hydrostatic pressure for the extension of their appendages, maintaining a posture with constant hydrostatic pressure with a small number of active muscles instead of the permanent use of all muscles with consequent metabolic activity (Carrel & Heathcote, 1976; Anderson & Prestwich, 1982). A low resting metabolic rate may be a factor that allows spiders to extend their survival without food (Tanaka & Ito,

1982; Canals *et al.*, 2007; Nentwig, 2013). In addition, spiders may reduce their metabolic rate significantly when they experience periods of food limitation (Ito, 1964; Miyashita, 1969; Anderson, 1974; Tanaka & Ito, 1982; Canals *et al.*, 2007; Phillip & Shillington, 2010; Stoltz *et al.*, 2010; Canals *et al.*, 2011).

Lighton *et al.* (2001) propose that spiders have metabolic rates similar to those of other land arthropods. They suggest that resting metabolic rate may be considered very conservative and that a general allometric rule between body mass and resting metabolic rate may be assessed for all land arthropods except for tarantulas (Araneae: Theraphosidae) (Shillington, 2002, 2005), as well as scorpions and ticks (Lighton *et al.*, 2001). However, there is a great diversity of spiders with different life styles. The suborder Mygalomorphae in general comprises primitive hunter wandering spiders, whereas the suborder Araneomorphae comprises the Haplogynae spiders that are primitive hunters and weavers, and also the Entelegynae, which includes the ‘modern’ spiders, such as the orb weaving spiders and the RTA clade (i.e. categorized by the presence of a retrolateral tibial apophysis) that tend to have more ‘energetically expensive’ life habits

Correspondence: Mauricio Canals, Departamento de Medicina and Programa de Salud ambiental, Escuela de Salud Pública, Facultad de Medicina, Universidad de Chile, Independencia 939, Postal Code 8380453, Santiago, Chile. Tel.: +56 2 9788596; e-mail: mcanals@uchile.cl

(Coddington & Levi, 1991; Penney *et al.*, 2003; Bell *et al.*, 2005; Kawamoto *et al.*, 2011).

Several studies fail to show metabolic differences that may be a consequence of ecological differences between different groups of spiders, other than those as a result of body mass, (Greenstone & Bennett, 1980; Anderson, 1994). For example, Anderson (1994), when analyzing species of the family Theridiidae with different life habits, reports differences that are only attributable to food restriction. However, Shillington (2005) reports higher resting metabolic rates in the more active males than females of the Texas tarantula *Aphonopelma anax*, suggesting that sexual differences in the habits of this spider could explain the metabolic differences. Similarly, Kawamoto *et al.* (2011) contradict the idea that spiders can be accepted as land arthropods in energetic terms (Lighton *et al.*, 2001) by showing allometric differences in resting metabolic rates between cribellate and cribellate orb weaver spiders, probably as a result of behavioural and activity differences associated with web building.

Based on measurements of low heart rate in primitive hunters and weaver spiders [Araneae: Loxoscelidae (Sicariidae) and Scytodidae], Carrel & Heathcote (1976) propose that these groups would have low metabolic rates, and suggest that this would be an energy-conserving adaptation in spiders that invest little effort in prey capture and, consequently, feed only occasionally. However, Greenstone & Bennett (1980) report no metabolic differences, other than those as a result of body mass, between spiders of the genus *Loxosceles* and other araneids. Carrel & Heathcote (1976) suggest that the almost constant ratio of 2.5 between heart rate and metabolism is indicative for Sicariidae and Scytodidae having low resting metabolic rates. By contrast, Greenstone & Bennett (1980) reject that idea and suggest that heart rate is an unreliable predictor of metabolic rate.

To resolve these conflicting views, the present study measures the rates of oxygen consumption and carbon dioxide release in the primitive hunters and weaver spiders, the Chilean Recluse *Loxosceles laeta* Nicolet (Araneae: Sicariidae) and Chilean Tiger *Scytodes globula* Nicolet (Araneae: Scytodidae), and analyses their relationship(s) with body mass, comparing the results with the metabolic data available for other primitive and nonprimitive spiders.

Materials and methods

Twenty-three individuals (13 females and 10 males) of *L. laeta* (average body mass = 127.55 ± 90.47 mg) and 26 individuals (16 females and 10 males) of *S. globula* (average body mass = 82.79 ± 51.74 mg) were captured during the autumn and spring inside houses of Santiago, Chile. The individuals were maintained in the laboratory for 2 weeks under an LD 12:12 h photocycle at ambient environmental temperature with food provided *ad libitum* consisting of *Tenebrio molitor* larvae. After a lapse of 1 day without a meal because the short specific dynamic action of spiders (Nespolo *et al.*, 2011), a first group of 14 individuals of *L. laeta* and 16 individuals of *S. globula*, as well as a second group of nine individuals of *L. laeta* and 10 of *S. globula*, were selected randomly and their oxygen consumption (\dot{V}_{O_2})

and carbon dioxide release (\dot{V}_{CO_2}) measured at 20 and 30 °C, respectively, during the day, which corresponds to the resting phase of both species (Alfaro *et al.*, 2013; Canals *et al.*, 2013, 2015). The respiratory quotient (RQ) was calculated as the ratio $\dot{V}_{CO_2} : \dot{V}_{O_2}$, and the temperature coefficient Q_{10} (i.e. metabolic change with the increase of 10 °C in temperature) was calculated using the ratio \dot{V}_{O_2} at 30 °C/ \dot{V}_{O_2} at 20 °C.

In the experiments, each individual was introduced into a sealed 20-mL syringe for 2 h inside a photo and thermoregulated cabinet. At the same time, two empty syringes were introduced into the same cabinet as controls. After 2 h, 50% of the volume of the syringe (10 mL) was introduced at a speed of 1 mL s^{-1} in an open continuous flow system, which aspired air with a flow $Q = 50 \text{ mL min}^{-1}$. Water was removed from the air by passage through columns of calcium sulphate anhydride (Drierite; WA Hammond Drierite Co., Ltd, Xenia, Ohio). Subsequently, the dry air was passed through a CO_2 trap, then filtered with barium hydroxide (Baralyme; Bionetics, Canada) and, finally, through the O_2 analyzer of a FOXBOX O_2 - CO_2 respirometry system (Sable Systems International, Las Vegas, Nevada). Data were corrected with respect to standard temperature and pressure and drift (baseline) and were analyzed using EXPEDATA, version 1.0.3 (Sable Systems International). The curves of O_2 and CO_2 were transformed to flow units (mL h^{-1}) with the relationships: $\dot{Q}_{O_2} = (-60 \cdot Q \cdot O_2 / 100) / (1 - 0.2095)$ and $\dot{Q}_{CO_2} = 60 \cdot Q \cdot CO_2 / 100$, respectively (Withers, 1977). The area under the curve: V_i , $i = O_2$ or CO_2 (mL) was measured, representing the total O_2 consumed and the total CO_2 released by the spiders. Then, O_2 consumption and CO_2 release were estimated as: $\dot{V}_i = 2(V_i - V_0) / t$, where V_0 corresponds to the average of the area under the curve of the two control syringes. The factor 2 originates from testing half of the volume, and t is the exact experimental time of each individual tested.

Statistical analysis

Metabolic variables were compared by two-way (species and temperatures) covariance analysis considering body mass as a covariate. The response variables were log transformed to satisfy normality and homoscedasticity assumptions studied with Shapiro–Wilk and Bartlett tests, respectively. Allometric relationships between oxygen consumption and body mass for both species were determined using regression analysis.

Comparative analysis

For comparative purposes, \dot{V}_{O_2} ($\mu\text{L g}^{-1} \text{h}^{-1}$) and \dot{V}_{CO_2} ($\mu\text{L g}^{-1} \text{h}^{-1}$) were measured at 20 °C in five individuals of *Dysdera crocata* (Araneae: Dysderidae) (mean body mass 122.92 ± 41.02 mg), as additional representatives of primitive hunters and weavers, as well as two individuals of *Pholcus phalangioides* (Araneae: Pholcidae) (mean body mass 82.78 ± 8.55 mg), a haplogynae spider species but representing web-weaving spiders (Bruvo-Madaric *et al.*, 2005). Also, the \dot{V}_{O_2} ($\mu\text{L g}^{-1} \text{h}^{-1}$) of several species of primitive hunters and weavers, comprising the present data on *L. laeta* and *S. globula*,

Table 1. Relationships between metabolic rate and body mass for arthropods (mass scaling equations) derived from various studies.

Original relationship	R _{EU}	Source of equation
$\text{Log}(\dot{V}_{\text{O}_2}; \mu\text{L h}^{-1}) = -0.133 + 0.710 \log(\text{Mb in mg})$	$\dot{V}_{\text{O}_2} = 736 M_b^{-0.29}$	Greenstone & Bennett (1980)
$\dot{V}_{\text{O}_2} (\mu\text{L g}^{-1} \text{h}^{-1}) = 947 M_b^{-0.408}$ (Mb in mg)	$\dot{V}_{\text{O}_2} = 947 M_b^{-0.408}$	Anderson (1974)
$M (\mu\text{W}) = 973 M_b^{0.856}$, M the metabolic rate and Mb in g	$\dot{V}_{\text{O}_2} = 452.5 M_b^{-0.144}$	Lighton <i>et al.</i> (2001)

R_{EU} represents the same relationships in equivalent units (\dot{V}_{O_2} in $\mu\text{L g}^{-1} \text{h}^{-1}$ and M_b in mg).

together with published data of the species *L. laeta*, *Loxosceles deserta* and *Plectreurys* spp. (Greenstone & Bennett, 1980) and *P. phalangioides* (present study), were compared with the data of various nonprimitive araneomorph spiders (Greenstone & Bennett, 1980) using covariance analysis. Only taxa with two or more data points were included. The primitive group included: Sicariidae (brown spiders), Scytodidae (spitting spiders), Dysderidae, Pholcidae (daddy long legs spiders) and Plectreuridae (plectreuid spiders) because these are among the most generalized of all the haplogyne ecribellate spiders (Gertsch, 1958). Group nonprimitive group included: Theridiidae (cobweb weavers), Lyniphiidae (sheetweb weavers), Araneidae (orb weavers), Agenelidae (funnel web weavers), Oxyopidae (lynx spiders), Thomisidae (crab spiders), Salticidae (jumping spiders), Lycosidae (wolf spiders) and Gnaphosidae and Clubionidae (sac spiders). Also, a cluster analysis was performed with the unweighted pair group method with arithmetic mean using \dot{V}_{O_2} ($\mu\text{L g}^{-1} \text{h}^{-1}$) as the response variable and the Euclidean distance. The phylogenetic relationships of the spiders used for comparisons were considered by measuring the phylogenetic signal in \dot{V}_{O_2} and performing phylogenetic contrast regressions based on phylogenetic hypotheses from Coddington & Levi (1991), Bell *et al.* (2005) and Penney *et al.* (2003).

Oxygen consumption values were compared with the expected values for respective body mass obeying mass scaling relationships according to the relationships of Greenstone & Bennett (1980) and Anderson (1994), as based on Carrel & Heathcote (1976) and Lighton *et al.* (2001) (Table 1).

Results

No differences were found in \dot{V}_{O_2} ($\mu\text{L g}^{-1} \text{h}^{-1}$) ($F_{1,42} = 0.28$, $P = 0.596$) or \dot{V}_{CO_2} ($\mu\text{L g}^{-1} \text{h}^{-1}$) ($F_{1,42} = 1.01$, $P = 0.319$) between the species *L. laeta* and *S. globula* in the present study. Also, there were no differences in \dot{V}_{O_2} ($\mu\text{L g}^{-1} \text{h}^{-1}$) or \dot{V}_{CO_2} ($\mu\text{L g}^{-1} \text{h}^{-1}$) between the sexes ($F_{1,42} = 2.40$, $P = 0.124$ and $F_{1,42} = 0.40$, $P = 0.53$, respectively) (Table 2).

Table 2. Oxygen consumption (\dot{V}_{O_2}), CO₂ release (\dot{V}_{CO_2}) and respiratory quotient (RQ) of primitive hunters and weaver spiders *Scytodes globula* and *Loxosceles laeta* at two temperatures.

Species	Experimental temperature (°C)	\dot{V}_{O_2} ($\mu\text{L g}^{-1} \text{h}^{-1}$)	\dot{V}_{CO_2} ($\mu\text{L g}^{-1} \text{h}^{-1}$)	RQ
<i>Scytodes globula</i>	20	92.22 ± 54.44	51.52 ± 18.46	0.71 ± 0.47
<i>Loxosceles laeta</i>	20	108.51 ± 108.60	63.01 ± 43.48	0.67 ± 0.33
<i>Scytodes globula</i>	30	177.82 ± 76.15	133.52 ± 41.41	0.74 ± 0.27
<i>Loxosceles laeta</i>	30	172.69 ± 124.00	85.95 ± 49.66	0.58 ± 0.24

Body mass affected both \dot{V}_{O_2} ($F_{1,42} = 9.56$, $P = 0.004$) and \dot{V}_{CO_2} ($F_{1,42} = 4.08$, $P = 0.049$). There was also an effect of experimental temperature on both \dot{V}_{O_2} ($F_{1,42} = 16.48$, $P = 0.0002$) and \dot{V}_{CO_2} ($F_{1,42} = 21.90$, $P = 0.00003$). There were no differences in the RQ between species ($F_{1,42} = 0.953$, $P = 0.335$) or between experimental temperatures ($F_{1,42} = 0.05$, $P = 0.82$).

Combining the oxygen consumption values of the two species at 20 °C, the relationships $\dot{V}_{\text{O}_2} = 573.85 \cdot M_b^{-0.46 \pm 0.27}$ and $\dot{V}_{\text{CO}_2} = 288.72 \cdot M_b^{-0.41 \pm 0.22}$ were obtained (with metabolic measurements in $\mu\text{L g}^{-1} \text{h}^{-1}$, and body mass in mg), although the regressions were not significant ($F_{1,26} = 2.84$, $P = 0.103$, $r^2 = 0.12$, and $F_{1,26} = 3.45$, $P = 0.075$, $r^2 = 0.10$ for \dot{V}_{O_2} and \dot{V}_{CO_2} , respectively) (Fig. 1). This can be explained by some spiders potentially showing activity inside the measurement syringe and because only a single measure of metabolic rate was undertaken.

For *D. crocata*, the \dot{V}_{O_2} and \dot{V}_{CO_2} were 97.18 ± 38.00 and $63.57 \pm 27.69 \mu\text{L g}^{-1} \text{h}^{-1}$, respectively; and, for *P. phalangioides*, the \dot{V}_{O_2} and \dot{V}_{CO_2} were 187.57 ± 15.79 and $110.66 \pm 34.43 \mu\text{L g}^{-1} \text{h}^{-1}$, respectively.

The mass-specific metabolic rates of *L. laeta* and *S. globula* were low compared with the expected (published) values for spiders and for arthropods of their body mass (Table 3). For example, \dot{V}_{O_2} values in the present study ($\mu\text{L g}^{-1} \text{h}^{-1}$) are 45.1% (*S. globula*) and 60.2% (for *L. laeta*) of the expected values, respectively, according to the mass scaling relationship derived from Greenstone & Bennett (1980), and 59.0% (*S. globula*) and 82.84% (*L. laeta*) of the expected values according to Anderson (1994). Using the average of the values of oxygen consumption at 20 and 30 °C as a proxy of oxygen consumption at 25 °C, \dot{V}_{O_2} ($\mu\text{L g}^{-1} \text{h}^{-1}$) estimates obtained in the present study were 56.4% (*S. globula*) and 63.5% (*L. laeta*), respectively, of the expected values derived from the mass scaling relationship of Lighton *et al.* (2001) (Table 3).

The \dot{V}_{O_2} ($\mu\text{L g}^{-1} \text{h}^{-1}$) in *D. crocata* was 53.3% of the expected value according to Greenstone & Bennett (1980) and 92.43% of the value according to Anderson (1994); the \dot{V}_{O_2} of *P. phalangioides* was 91.7% of the expected value from Greenstone &

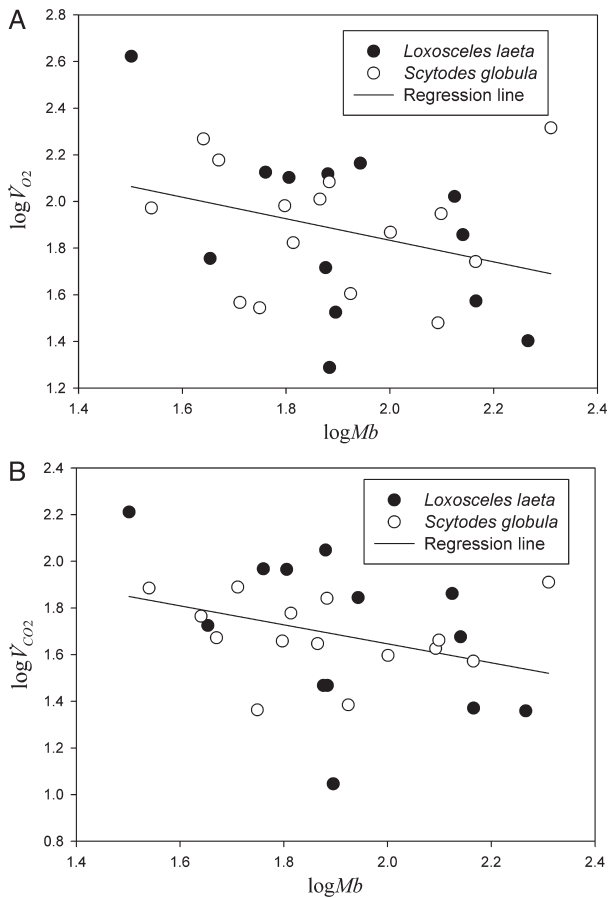


Fig. 1. (A) Log-log relationship of oxygen consumption (\dot{V}_{O_2} ; $\mu\text{L g}^{-1} \text{h}^{-1}$) and body mass of primitive hunters and weaver spiders *Scytodes globula* and *Loxosceles laeta* at 20°C. (B) Log-log relationship of CO₂ release (\dot{V}_{CO_2} ; $\mu\text{L g}^{-1} \text{h}^{-1}$) and body mass (mg) of *S. globula* and *L. laeta* at 20°C.

Bennett (1980) and 120.04% of the derived value from Anderson (1994). In these cases, the expected values according to the mass scaling relationship from Lighton *et al.* (2001) were not calculated because this relationship is for arthropods at 25°C.

The average \dot{V}_{O_2} ($\mu\text{L g}^{-1} \text{h}^{-1}$) at 20°C of the primitive group (all measurements) was lower than that of the nonprimitive group ($F_{1,76} = 3.91$, $P = 0.05$), although without differences in the slopes ($F_{1,76} = 0.94$, $P = 0.13$). A weak but significant phylogenetic signal in \dot{V}_{O_2} ($\mu\text{L g}^{-1} \text{h}^{-1}$) was found (Moran's $I = 0.034$, $P = 0.02$). Cluster analysis showed that, from a metabolic point of view, there are three clusters: (i) Dysderidae–Sicariidae–Clubionidae–Plectreuridae–Scytodidae–Gnaphosidae; (ii) Pholcidae–Thomisidae–Agelenidae–Lycosidae–Oxiopidae–Salticidae–Araneidae; and (iii) Lynphiidae–Theridiidae. The first cluster includes mainly primitive hunters and weaver spiders and the second and third clusters include active predators and web weaving spiders (Fig. 2). Analyzing \dot{V}_{O_2} ($\mu\text{L g}^{-1} \text{h}^{-1}$) as a function of body mass in all spiders yields a slope: -0.248 ± 0.146 ($F_{1,13} = 2.88$, $P = 0.11$). The slope is similar when excluding primitive spiders: -0.224 ± 0.123 ($F_{1,9} = 3.31$, $P = 0.10$). When correcting by phylogeny, the

Table 3. Comparison of the expected values of \dot{V}_{O_2} ($\mu\text{L g}^{-1} \text{h}^{-1}$) for the primitive hunters and weaver spiders in the present study assuming the mass scaling relationships by Greenstone & Bennett (1980) and Anderson (1994), as based on Carrel & Heathcote, 1976) and Lighton *et al.* (2001), respectively (the observed/estimated ratios obtained experimentally are shown in parenthesis).

Species	Greenstone & Bennett (1980)	Anderson (1994)	Lighton <i>et al.</i> (2001)
<i>Loxosceles laeta</i>	180.40 (60.15)	130.99 (82.84)	225.13 (62.45)*
<i>Scytodes globula</i>	204.49 (45.09)	156.25 (59.02)	239.58 (56.36)*
<i>Dysdera crocata</i>	182.34 (53.30)	132.98 (73.08)	—
<i>Pholcus phalangioides</i>	204.49 (91.72)	156.26 (120.04)	—

Asterisks indicate that, in these cases, the experimental \dot{V}_{O_2} was calculated as the average between metabolic values at 20 and 30°C.

general allometric tendency was maintained as indicated by the slope: -0.246 ± 0.132 ($F_{1,13} = 3.45$, $P = 0.08$) (Fig. 3).

Discussion

The resting metabolic rates of the primitive hunters and weaver spiders *L. laeta*, *S. globula* and *D. crocata* are lower (by approximately 60%) than expected for their body mass, regardless of the allometric relationship used in the comparisons. As in other spiders, this could be explained by the use of hydrostatic pressure to maintain body posture instead of the energetically expensive utilization of all muscles (Carrel & Heathcote, 1976; Anderson & Prestwich, 1982; Wilder, 2011). Another explanation for the lower rates of metabolism could be the smaller number of mitochondria in the muscle fibres of spiders (Linzen & Gallowitz, 1975). This low level of resting metabolic rate may be an important factor that allows certain species to survive and save energy for long periods without food (Anderson, 1974; Tanaka & Ito, 1982; Nentwig, 2013). Also, spiders are able to reduce their metabolic rates to lower values than usual during periods of food restriction, which can reach values close to 50% of those for a well-fed spider (Ito, 1964; Miyashita, 1969; Anderson, 1974; Tanaka & Ito, 1982; Canals *et al.*, 2007; Stoltz *et al.*, 2010; Canals *et al.*, 2011).

Most spiders are able to raise their metabolism above the resting rates by two- to six-fold (Anderson & Prestwich, 1982; Prestwich, 1983a, 1983b; Nespolo *et al.*, 2011; Canals *et al.*, 2012); however, web building spiders may increase their metabolic rate above resting levels by almost ten- to 20-fold when building a web (Wilder, 2011).

Discounting the effect of the body mass, the present study finds no effect of sex on the resting metabolic rate; however, other studies report differences attributable to high energetic requirements of males during the reproductive period (Watson & Lighton, 1994; Kotiaho, 1998; Uetz *et al.*, 2002; Lomborg & Toft, 2009). This may be explained by the fact that spiders are analyzed during the nonbreeding season in the present study.

The estimates of Q_{10} reported in the present study are not measured directly in the analyzed species because the individuals measured at 20°C are different from those measured at 30°C, and the Q_{10} reflects the capacity of change in metabolic rate relative to changes in temperature, considered as an individual

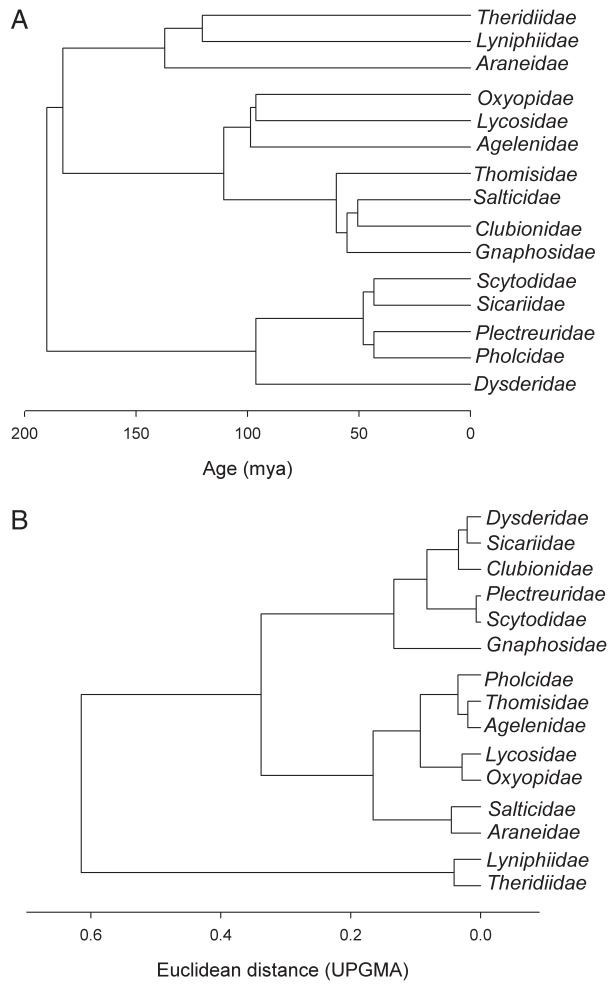


Fig. 2. (A) Phylogenetic relationships of the spider families considered for metabolic comparisons. Based on Coddington & Levi (1991), Bell *et al.* (2005) and Penney *et al.* (2003). (B) Cluster analysis of \dot{V}_{O_2} ($\mu\text{L g}^{-1} \text{h}^{-1}$) in these spider families based on the unweighted pair group method with arithmetic mean and Euclidean distances.

attribute (Nespolo *et al.*, 2003). Nevertheless, broad estimates of Q_{10} in the present study are derived from the ratio of \dot{V}_{O_2} between 30 and 20 °C and ratio of \dot{V}_{CO_2} between 30 and 20 °C. These are 1.92 and 2.59 for *S. globula* and 1.59 and 1.36 for *L. laeta*, respectively. Values ranging from 1.35 to 3 are reported in various arachnids and insects (Anderson, 1970; Prestwich & Walker, 1981; Ashby, 1997; Davis *et al.*, 1999; Rogowitz & Chappell, 2000; Rourke, 2000; Schmitz & Perry, 2001).

The RQ value measured in the present study is approximately 0.7 in *L. laeta* and *S. globula*, suggesting the metabolism of predominantly lipids, as expected according to the prey offered during the pre-experimental period and according to the prey that these spiders usually eat (small arthropods).

The \dot{V}_{O_2} of *D. crocata* is also low, and similar to of the values for *S. globula* and *L. laeta*. However, the \dot{V}_{O_2} of *P. phalangioides* is approximately equal or even superior to that expected for its body mass. Despite the high \dot{V}_{O_2} in *P. phalangioides*, the comparison made between primitive and nonprimitive groups

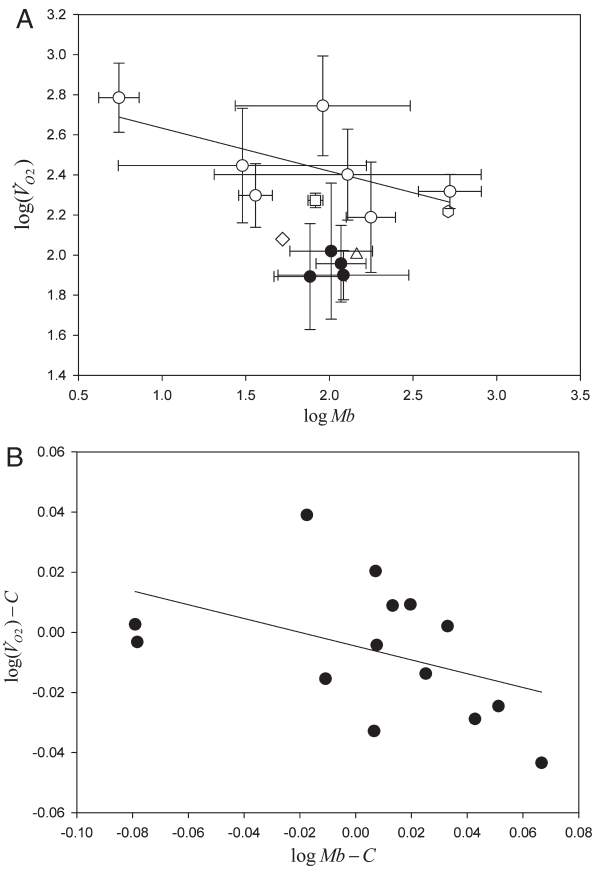


Fig. 3. (A) Log-log relationship of oxygen consumption (\dot{V}_{O_2} ; $\mu\text{L g}^{-1} \text{h}^{-1}$) and body mass (mg) of spider families (Primitive and nonprimitive groups) at 20 °C. Only taxa with two or more points were included in the regression analysis of groups. The nonprimitive group (white circles and line) comprises Theridiidae (cobweb weavers), Lynphiidae (sheetweb weavers), Araneidae (orb weavers), Agelenidae (funnel web weavers), Oxyopidae (lynx spiders), Thomisidae (crab spiders) and Salticidae (jumping spiders). The primitive group (black circles, without line) because it was not significant) included Sicariidae (brown spiders), Scytodidae (spitting spiders), Dysderidae and Plectreuridae. Points from spider families not included in regression analyses comprise Lycosidae (white hexagon), Pholcidae (white square), Gnaphosidae (white rhombus) and Clubionidae (white triangle). (B) Phylogenetic contrast of log-log relationship of oxygen consumption (\dot{V}_{O_2} ; $\mu\text{L g}^{-1} \text{h}^{-1}$) and body mass (mg) of all primitive and nonprimitive groups of spider families at 20 °C.

finds that primitive hunters and weaver spiders have a resting metabolic rate lower than the nonprimitive group, in agreement with the hypothesis of Carrel & Heathcote (1976), which is based on the low heart rate of species of the Scytodidae and Sicariidae families compared with eight other araneomorph spider families. This lower basal metabolic rate in primitive hunters and weaver spiders may have evolved in association with their life style and, in particular, their sit and wait predatory strategy in unpredictable environments with low prey availability, similar to that proposed for mygalomorph spiders (Greenstone & Bennett, 1980; Shillington, 2002; Canals *et al.*, 2007, 2011). It is interesting that Greenstone & Bennett (1980) reject the

hypothesis of Carrel & Heathcote (1976), arguing that heart rate is a bad predictor of metabolism. However, the findings from the present study are in agreement with Carrel & Heathcote (1976), even when including the nine values for *L. laeta* and two for *L. deserta* from the study by Greenstone & Bennett (1980) together with the present data. Also, the results for *L. laeta* (mean \dot{V}_{O_2} at 20°C; $\mu\text{L}\cdot\text{h}^{-1}\cdot\text{g}^{-1}$) from the present study are not different from those of Greenstone & Bennett (1980): 108.51 ± 108.60 (present study) versus 138.52 ± 34.52 (Greenstone & Bennett, 1980), respectively. This implies that the differences between the conclusions of the present study and that of Greenstone & Bennett (1980) are not explained by differences in metabolic rate values but rather by the increased sample size of spiders analyzed.

The present study detects a weak phylogenetic signal in the metabolic rate, which may be explained by the primitive group being composed of only Haploginae spiders. These are mainly primitive spiders with low fertility (Fernandez *et al.*, 2002; Canals & Solís, 2014) and low energetic cost strategies compared with the nonprimitive group that includes spiders of the RTA clade and orbweb spiders that are characterized by high energetic costs of web building and high fertility (Blackledge *et al.*, 2009). Cluster analysis not only shows that all haplogynae spiders (excepting Pholcidae) are clustered in a single group, but also that the 'entelegyneae sac' spiders (Clubionidae) and ground spiders (Gnaphosidae) are included in this group. Sac spiders are nocturnal species that forage on the ground or in the foliage, and that build a compact silk retreat each morning before becoming inactive for rest of the day time. The ground spiders hunt on the ground and do not build a capture web (Bradley, 2013). Combined together, this single cluster may be considered as a group of primitive hunters and weaver spiders. Also, it is interesting to note that *P. phalangoides*, a haplogynae but web weaving spider (that is included in the primitive group in the present study) shows a higher oxygen consumption than *S. globula*, the Plectreuridae and the other close family relatives of the primitive group (Coddington & Levi, 1991; Penney *et al.*, 2003; Bell *et al.*, 2005; Blackledge *et al.*, 2009) but a consumption similar to that of the spiders of the nonprimitive group. This could suggest a higher metabolism associated with web building.

The results of the present study reject the proposition of Lighton *et al.* (2001), who suggest a general relationship for all land arthropods except ticks and scorpions, and the results are also in agreement with other studies reporting different metabolic rates (Kawamoto *et al.*, 2011) and fertility differences (Blackledge *et al.*, 2009), reflecting a different strategy in energy allocation between ecribellate and cribellate spiders. Also, the results of the present study agree with the low energy strategy reported for the Theraphosidae, which show metabolic rates lower than those expected by their body mass. In addition, the findings of the present study agree with the hypothesis of Carrel & Heathcote (1976), suggesting that metabolic rates are affected not only by sex, reproductive and developmental status, but also by ecology and life style, recognizing, at least in the araneomorph spiders, a group having low metabolism, comprising the primitive hunters and weavers, and another group comprising the web building spiders.

Acknowledgements

We thank Lafayette Eaton for his review of the English and helpful comments on the manuscript submitted for publication. The present study was funded by a FONDECYT 1110058 grant to M.C.

References

- Alfaro, C., Veloso, C., Torres-Contreras, H. *et al.* (2013) Thermal niche overlap of the brown recluse spider *Loxosceles laeta* (Araneae; Sicariidae) and its possible predator, the spitting spider *Scytodes globula* (Scytodidae). *Journal of Thermal Biology*, **38**, 502–507.
- Anderson, J.F. (1970) Metabolic rates of spiders. *Comparative Biochemistry and Physiology*, **33**, 51–72.
- Anderson, J.F. (1974) Responses to starvation in the spiders *Lycosa lenta* (Hentz) and *Filistata hibernalis* (Hentz). *Ecology*, **55**, 576–585.
- Anderson, J.F. (1994) Comparative energetics of comb-footed spiders (Araneae: theridiidae). *Comparative Biochemistry and Physiology Part A, Comparative Physiology*, **109**, 181–189.
- Anderson, J.F. & Prestwich, K.N. (1982) Respiratory gas exchange in spiders. *Physiological Zoology*, **55**, 72–90.
- Ashby, P.D. (1997) Conservation of mass-specific metabolic rate among high- and low- elevation populations of the acridid grasshopper *Xanthippus corallipes*. *Physiological and Biochemical Zoology*, **70**, 701–711.
- Bell, J.R., Bohan, D.A., Shaw, D.M. & Weyman, G.S. (2005) Ballooning dispersal using silk: world fauna, phylogenies, genetics and models. *Bulletin of Entomological Research*, **95**, 69–114.
- Blackledge, T.A., Coddington, J.A. & Agnarsson, I. (2009) Fecundity increase supports adaptive radiation hypothesis in spider web evolution. *Communicative & Integrative Biology*, **2**, 459–463.
- Bradley, R.A. (2013) *Common Spiders of North America*. University of California Press, Berkeley, California.
- Bruvo-Madaric, B., Huber, B.A., Steinacher, A. & Pass, G. (2005) Phylogeny of pholcid spiders (Araneae: Pholcidae): combined analysis using morphology and molecules. *Molecular Phylogenetics and Evolution*, **37**, 661–673.
- Canals, M. & Solís, R. (2014) Desarrollo de cohortes y parámetros poblacionales de la araña del rincón *Loxosceles laeta*. *Revista Chilena de Infectología*, **31**, 547–554.
- Canals, M., Salazar, M.J., Durán, C. *et al.* (2007) Respiratory refinements in the mygalomorph spider *Grammostola rosea* Walckenaer 1837 (Araneae, Theraphosidae). *Journal of Arachnology*, **35**, 481–486.
- Canals, M., Figueroa, D., Alfaro, C. *et al.* (2011) Effects of diet and water supply on energy intake and water loss in a mygalomorph spider in a fluctuating environment of the central Andes. *Journal of Insect Physiology*, **57**, 1489–1494.
- Canals, L., Figueroa, D.P., Torres-Contreras, H. *et al.* (2012) Mealworm (*Tenebrio molitor*) diets relative to the energetic requirements of small mygalomorph spiders (*Paraphysa* sp.). *Journal of Exotic Pet Medicine*, **21**, 203–206.
- Canals, M., Alfaro, C., Veloso, C. *et al.* (2013) Tolerancia a la desecación y sobreposición del nicho térmico entre la araña del rincón *Loxosceles laeta* y un posible control biológico, la araña tigre *Scytodes globula*. *Parasitología Ibero-Latinoamericana*, **72**, 52–60.
- Canals, M., Arriagada, N. & Solís, R. (2015) Interactions between the Chilean recluse spider and an araneophagic spitting spider. *Journal of Medical Entomology*, **52**, 109–116.
- Carrel, J.E. & Heathcote, R.D. (1976) Heart rate in spiders: influence of body size and foraging energetic. *Science*, **193**, 148–150.

- Coddington, J.A. & Levi, H.W. (1991) Systematics and evolution of spiders (Araneae). *Annual Review of Ecology and Systematics*, **22**, 443–447.
- Davis, A.L.V., Chown, S.L. & Scholtz, C.H. (1999) Discontinuous gas exchange cycles in *Scarabelus* dung beetles (Coleoptera: Scarabaeidae): mass-scaling and temperature dependence. *Physiological Biochemistry and Zoology*, **72**, 555–565.
- Fernandez, D., Ruz, L. & Toro, H. (2002) Aspectos de la biología de *Scytodes globula* Nicolet, 1949 (Araneae: Scytodidae), un activo depredador de Chile Central. *Acta Entomologica Chilena*, **26**, 17–25.
- Gertsch, W.J. (1958) The spider family Plectreuridae. *American Museum Novitates*, **1920**, 1–53.
- Greenstone, M.H. & Bennett, A.F. (1980) Foraging strategy and metabolic rate in spiders. *Ecology*, **61**, 1255–1259.
- Ito, Y. (1964) Preliminary studies on the respiratory energy loss of a spider, *Lycosa pseudoannulata*. *Researches on Population Ecology*, **6**, 13–21.
- Kawamoto, T.H., Machado, F.de.A., Kaneto, G.E. & Japyassú, H.F. (2011) Resting metabolic rates of two orbweb spiders: a first approach to evolutionary success of ecribellate spiders. *Journal of Insect Physiology*, **57**, 427–532.
- Kotiaho, J.S. (1998) Sexual differences in metabolic rates of spiders. *The Journal of Arachnology*, **26**, 401–404.
- Lighton, J.R.B., Brownell, P.H., Joos, B. & Turner, R.J. (2001) Low metabolic rate in scorpions: implications for population biomass and cannibalism. *The Journal of Experimental Biology*, **204**, 607–613.
- Linzen, B. & Gallowitz, P. (1975) Enzyme activity patterns of muscles of the lycosid spider *Cupiennius saliei*. *Journal of Comparative Physiology*, **96**, 101–109.
- Lomborg, J.P. & Toft, S. (2009) Nutritional enrichment increases courtship intensity and improves mating success in male spiders. *Behavioral Ecology*, **20**, 700–708.
- Miyashita, K. (1969) Effects of locomotory activity, temperature and hunger on the respiratory rate of *Lycosa T-insignata* Boes et Str (Araneae: Lycosidae). *Applied Entomology and Zoology*, **4**, 105–113.
- Nentwig, W. (2013) *Spider Ecophysiology*. Springer-Verlag, Germany.
- Nespolo, R., Lardies, M.A. & Bozinovic, F. (2003) Intrapopulation variation in the standard metabolic rate of insects: repeatability, thermal dependence and sensitivity (Q_{10}) of oxygen consumption in a cricket. *Journal of Experimental Biology*, **206**, 4309–4315.
- Nespolo, R., Correa, L., Pérez-Apablaza, C.X. et al. (2011) Energy metabolism and the postprandial response of the Chilean tarantulas. *Euathlus truculentus* (Araneae, Theraphosidae). *Comparative Biochemistry and Physiology Part A*, **159**, 379–382.
- Penney, D., Wheeler, C.P. & Selden, P.A. (2003) Resistance of spiders to Cretaceous–Tertiary extinction events. *Evolution*, **57**, 2599–2607.
- Phillip, B.N. & Shillington, C. (2010) The effect of prey availability on metabolism and activity in the tarantula *Phormictopus cancerides*. *Canadian Journal of Zoology*, **88**, 90–98.
- Prestwich, K.N. (1983a) The roles of aerobic and anaerobic metabolism in active spiders. *Physiological Zoology*, **56**, 122–132.
- Prestwich, K.N. (1983b) Anaerobic metabolism in spiders. *Physiological Zoology*, **56**, 112–121.
- Prestwich, K.N. & Walker, T.J. (1981) Energetics of singing in crickets: effect of temperature in three trilling species (Orthoptera: Gryllidae). *Oecologia*, **143**, 199–212.
- Rogowitz, G.L. & Chappell, M.A. (2000) Energy metabolism of eucalyptus-boring beetles at rest and during locomotion: gender makes a difference. *Journal of Experimental Biology*, **203**, 1131–1139.
- Rourke, B. (2000) Geographic and altitudinal variation in water balance and metabolic rate in a California grasshopper, *Melanoplus sanguinipes*. *Journal of Experimental Biology*, **203**, 2699–2712.
- Schmitz, A. & Perry, S.F. (2001) Bimodal breathing in jumping spiders: morphometric partition of the lungs and trachea in *Salticus scenicus* (Arachnida, Araneae, Salticidae). *Journal of Experimental Biology*, **204**, 4321–4334.
- Shillington, C. (2002) Thermal ecology of male tarantulas (*Aphonopelma anax*) during the mating season. *Canadian Journal of Zoology*, **80**, 251–259.
- Shillington, C. (2005) Inter-sexual differences in resting metabolic rates in the Texas tarantula, *Aphonopelma anax*. *Comparative Biochemistry and Physiology Part A*, **142**, 439–445.
- Stoltz, J.A., Hanna, R. & Andrade, M.C.B. (2010) Longevity costs of remaining unmated under dietary restriction. *Functional Ecology*, **24**, 1270–1280.
- Tanaka, K. & Ito, Y. (1982) Decrease in respiratory rate in a wolf spider, *Pardosa astrigera*, under starvation. *Researches on Population Ecology*, **24**, 360–374.
- Uetz, G.W., Papke, R. & Kilinc, B. (2002) Influence of feeding regime on body size, body condition and a male secondary sexual character in *Schizocosa ocreata* wolf spiders (Araneae, Lycosidae): condition-dependence in a visual signaling trait. *The Journal of Arachnology*, **30**, 461–469.
- Watson, P.J. & Lighton, J.R.B. (1994) Sexual selection and the energetics of copulatory courtship in the Sierra dome spider, *Linyphia litigiosa*. *Animal Behavior*, **48**, 615–626.
- Wilder, S.M. (2011) Spider nutrition: an integrative perspective. *Advances in Insect Physiology*, **40**, 87–136.
- Withers, P.C. (1977) Measurements of V_{O_2} , V_{CO_2} , and evaporative water loss with a flow-through mask. *Journal of Applied Physiology*, **42**, 120–123.

Accepted 9 June 2015

First published online 6 July 2015