Low metabolic rates in primitive hunters and weaver spiders

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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.
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 (Lighthon et al., 2001) by showing allometric differences in resting metabolic rates between ecribellate 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 photolytic cycle 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 ($V_{O2}$) and carbon dioxide release ($V_{CO2}$) 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 $V_{CO2} / V_{O2}$, and the temperature coefficient $Q_{10}$ (i.e. metabolic change with the increase of 10 °C in temperature) was calculated using the ratio $V_{O2}$ at 30 °C/$V_{O2}$ at 20 °C.

In the experiments, each individual was introduced into a sealed 20-mL syringe for 2 h in 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 aspirated air with a flow $Q = 50$ 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 expeddata, 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: $Q_{O2} = (-60 · Q·O2/100)/(1 − 0.2095)$ and $Q_{CO2} = 60·Q·CO2/100$, respectively (Withers, 1977). The area under the curve: $V_v$, where $V_v$ 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, $V_{O2}$ (µL·g$^{-1}$·h$^{-1}$) and $V_{CO2}$ (µL·g$^{-1}$·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 haplogyne spider species but representing web-weaving spiders (Bruvo-Madaric et al., 2005). Also, the $V_{O2}$ (µL·g$^{-1}$·h$^{-1}$) of several species of primitive hunters and weavers, comprising the present data on L. laeta and S. globula,
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Table 1. Relationships between metabolic rate and body mass for arthropods (mass scaling equations) derived from various studies.

<table>
<thead>
<tr>
<th>Original relationship</th>
<th>( R_{EU} )</th>
<th>Source of equation</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \log(\dot{V}_{O2}; \mu L \cdot h^{-1}) = -0.133 + 0.710 \log(\text{Mb in mg}) )</td>
<td>( \dot{V}_{O2} = 736 \text{Mb}^{-0.29} )</td>
<td>Greenstone &amp; Bennett (1980)</td>
</tr>
<tr>
<td>( \dot{V}_{O2} (\mu L \cdot g^{-1} \cdot h^{-1}) = 947 \text{Mb}^{-0.48} )</td>
<td>( \dot{V}_{O2} = 947 \text{Mb}^{-0.406} )</td>
<td>Anderson (1974)</td>
</tr>
<tr>
<td>( M (\mu W) = 973 \text{Mb}^{0.856}, M ) the metabolic rate and ( \text{Mb} ) in g</td>
<td>( \dot{V}_{O2} = 452.5 \text{Mb}^{-0.144} )</td>
<td>Lighton et al. (2001)</td>
</tr>
</tbody>
</table>

\( R_{EU} \) represents the same relationships in equivalent units (\( \dot{V}_{O2} \) in \( \mu L \cdot h^{-1} \) and \( \text{Mb} \) in mg).

Together with published data of the species \( L. \) laeta, \( Loxosceles \) deserta and \( Plectreurys \) spp. (Greenstone & Bennett, 1980) and \( P. \) palangioides (present study), were compared with the data of various nonprimitive arachnoid 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 (plectreurid spiders) because these are among the most generalized of all the haploxygene ecrabilate spiders (Gertsch, 1958). Group nonprimitive group included: Theridiidae (cobweb weavers), Lynipiidae (sheetweb weavers), Araneidae (orb weavers), Ageniidae (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 \( \dot{V}_{O2} \) (\( \mu L \cdot g^{-1} \cdot h^{-1} \)) 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 \( \dot{V}_{O2} \) 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 \( \dot{V}_{O2} \) (\( \mu L \cdot g^{-1} \cdot h^{-1} \)) (\( F_{1,42} = 0.28, P = 0.596 \)) or \( \dot{V}_{CO2} \) (\( \mu L \cdot g^{-1} \cdot h^{-1} \)) (\( F_{1,42} = 1.01, P = 0.319 \)) between the species \( L. \) laeta and \( S. \) globula in the present study. Also, there were no differences in \( \dot{V}_{O2} \) (\( \mu L \cdot g^{-1} \cdot h^{-1} \)) or \( \dot{V}_{CO2} \) (\( \mu L \cdot g^{-1} \cdot h^{-1} \)) between the sexes (\( F_{1,42} = 2.40, P = 0.124 \) and \( F_{1,42} = 0.40, P = 0.53 \), respectively) (Table 2).

Body mass affected both \( \dot{V}_{O2} \) (\( F_{1,42} = 9.56, P = 0.004 \)) and \( \dot{V}_{CO2} \) (\( F_{1,42} = 4.08, P = 0.049 \)). There was also an effect of experimental temperature on both \( \dot{V}_{O2} \) (\( F_{1,42} = 16.48, P = 0.0002 \)) and \( \dot{V}_{CO2} \) (\( F_{1,42} = 21.90, P = 0.0003 \)). 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 \( \dot{V}_{O2} = 573.85 \text{Mb}^{-0.462} \) and \( \dot{V}_{CO2} = 288.72 \text{Mb}^{-0.412} \) were obtained (with metabolic measurements in \( \mu L \cdot g^{-1} \cdot h^{-1} \), 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 \( \dot{V}_{O2} \) and \( \dot{V}_{CO2} \), 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 \( \dot{V}_{O2} \) and \( \dot{V}_{CO2} \) were 97.18 ± 38.00 and 63.57 ± 27.69 \( \mu L \cdot g^{-1} \cdot h^{-1} \), respectively; and, for \( P. \) phalangioides, the \( \dot{V}_{O2} \) and \( \dot{V}_{CO2} \) were 187.57 ± 15.79 and 110.66 ± 34.43 \( \mu L \cdot g^{-1} \cdot h^{-1} \), 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, \( \dot{V}_{O2} \) values in the present study (\( \mu L \cdot g^{-1} \cdot h^{-1} \)) 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, \( \dot{V}_{O2} \) (\( \mu L \cdot g^{-1} \cdot h^{-1} \)) 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 \( \dot{V}_{O2} \) (\( \mu L \cdot g^{-1} \cdot h^{-1} \)) 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 \( \dot{V}_{O2} \) of \( P. \) phalangioides was 91.7% of the expected value from Greenstone &

Table 2. Oxygen consumption (\( \dot{V}_{O2} \)), CO2 release (\( \dot{V}_{CO2} \)) and respiratory quotient (RQ) of primitive hunters and weaver spiders \( Scytodes \) globula and \( Loxosceles \) laeta at two temperatures.

<table>
<thead>
<tr>
<th>Species</th>
<th>Experimental temperature (°C)</th>
<th>( \dot{V}_{O2} ) (( \mu L \cdot g^{-1} \cdot h^{-1} ))</th>
<th>( \dot{V}_{CO2} ) (( \mu L \cdot g^{-1} \cdot h^{-1} ))</th>
<th>RQ</th>
</tr>
</thead>
<tbody>
<tr>
<td>Scytodes globula</td>
<td>20</td>
<td>92.22 ± 54.44</td>
<td>51.52 ± 18.46</td>
<td>0.71 ± 0.47</td>
</tr>
<tr>
<td>Loxosceles laeta</td>
<td>20</td>
<td>108.51 ± 108.60</td>
<td>63.01 ± 43.48</td>
<td>0.67 ± 0.33</td>
</tr>
<tr>
<td>Scytodes globula</td>
<td>30</td>
<td>177.82 ± 76.15</td>
<td>133.52 ± 41.41</td>
<td>0.74 ± 0.27</td>
</tr>
<tr>
<td>Loxosceles laeta</td>
<td>30</td>
<td>172.69 ± 124.00</td>
<td>85.95 ± 49.66</td>
<td>0.58 ± 0.24</td>
</tr>
</tbody>
</table>

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
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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 $\dot{V}_{O_2}$ ($\mu$L g$^{-1}$ 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 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

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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 V_o2 at 20 °C; μLh^-1g^-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 Haplognae 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 (Gnaphosidea) 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 Plecturiridae 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 ecribelle 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.

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