Resting metabolic rates of two orbweb spiders: A first approach to evolutionary success of ecribellate spiders

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ABSTRACT

Spiders are considered conservative with regard to their resting metabolic rate, presenting the same allometric relation with body mass as the majority of land-arthropods. Nevertheless, web-building is thought to have a great impact on the energetic metabolism, and any modification that affects this complex behavior is expected to have an impact over the daily energetic budget. We analyzed the possibility of the presence of the cribellum having an effect on the allometric relation between resting metabolic rate and body mass for an ecribellate species (*Zosis geniculata*) and a cribellate one (*Metazygia rogenhoferi*), and employed a model selection approach to test if these species had the same allometric relationship as other land-arthropods. Our results show that *M. rogenhoferi* has a higher resting metabolic rate, while *Z. geniculata* fitted the allometric prediction for land arthropods. This indicates that the absence of the cribellum is associated with a higher resting metabolic rate, thus explaining the higher promptness to activity found for the ecribellate species. If our result proves to be a general rule among spiders, the radiation of Araneoidea could be connected to a more energy-consuming life style. Thus, we briefly outline an alternative model of diversification of Araneoidea that accounts for this possibility.

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1. Introduction

All living organisms use many energy-consuming processes to stay alive and reproduce. On the one hand, metabolic rates vary with changes of environmental and physiological conditions; on the other hand, metabolic rates pose limits to physiological changes and environmental interactions. In this way, metabolic rates have important ecological and evolutionary consequences (Garland and Carter, 1994; Chown, 2001), and have often been evoked in discussions about physiological ecology and evolutionary physiology (Reinhold, 1999).

Spiders are typically sit-and-wait foragers remaining motionless most of the time, a condition which stresses the importance of the resting metabolic rate in their life cycle. Food availability limits and shapes the ecology and behavior of spiders (Wise, 1993), affecting several life history traits such as reproduction (Eberhard, 1979), web building (Pasquet et al., 1994; Sandoval, 1994), sociality (Rypstra, 1985; Kim, 2000) and growth (Vollrath, 1985). Spiders may have evolved adaptations to unpredictable and low prey availability (Greenstone and Bennett, 1980), a condition that would perfectly match their alleged low resting metabolic rates (Anderson, 1970). However, Lighton et al. (2001) argued that spiders actually have a metabolism that is very similar to that of other land-arthropods. Overall, it was shown that the arthropod resting metabolic rate could be considered extremely conservative, and that a general allometric rule between body mass and resting metabolic rate could be modeled for all land arthropods, except for tarantulas (Shillington, 2005), scorpions and ticks (Lighton et al., 2001).

One important source of effects on energetic metabolism is the execution of energetically costly behaviors (Reinhold, 1999), an aspect particularly neglected in the study of spider physiology.

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Despite the fact that spiders are sit-and-wait foragers, a typical economic foraging strategy as mentioned above, they are able to exhibit some behaviors with important impacts in their daily energetic budget (Watson and Lighton, 1994). Among web weavers, the web building behavior is the main energetic expenditure, thus any modification that affects the cost of web building should be expected to have metabolic impact on the organism, probably influencing the energetic budget and other significant aspects of the spiders' life, such as reproduction and survival rate (Angilletta et al., 2003). The loss of the cribellate silk is probably one of these modifications.

The cribellum is a modification of the anterior median spinnerets into one or two small flat plates densely covered with tiny spigots which, together with the calamistrum, a row of strong bristles on the metatarsus of leg IV, produce the cribellate silk (Foelix, 1996). Even though the cribellate spiders were originally considered a separate group which followed an evolutionary path parallel to ecribellate spiders, resulting in numerous convergences (Shear, 1986), recent phylogenetic studies have shown that the cribellum is, in fact, plesiomorphic for all extant spiders and most groups exhibit a secondary loss of this character (Lehtinen, 1967; Coddington and Levi, 1991; Griswold et al., 1999). The production of the cribellate orbweb is more expensive than the production of an ecribellate orbweb: while ecribellate webs are adhesive due to an aqueous, diluted glue, the cribellate silk is constituted of numerous tiny proteic fibrils that need to be repeatedly "combed" in order to produce the capture spiral (Peters, 1987). Cribellate spiders also reingest their webs less frequently than ecribellate orb weavers. Indeed, it was shown that there is a significant difference in energy economy of web building and maintenance of viscid orbwebs when compared to cribellate orbwebs (e.g. Opell, 1996, 1998). Finally, cribellate spiders seem to be more reluctant to abandon their webs than ecribellate spiders, even when submitted to low prey availability, suggesting that the energetic and behavioral commitment to web building is greater in cribellate animals (Kawamoto, 2007; Kawamoto and Japyassú, 2007).

In the present work we investigate the possibility that the behavioral and physiological differences associated with the presence or absence of the cribellum have an effect on the resting metabolic rate of spiders. In order to do that we measured resting metabolism and body mass of a cribellate and an ecribellate species, and employed a model selection approach to explore the allometric relation between these variables compared to the prediction for land arthropods (Lighton et al., 2001). Finally, we briefly discuss the relevance of our findings to the understanding of diversity within the clade of orbweavers. Ecribellate orbweavers (Araneoidea) comprise 27.8% of the total number of spider species (Platnick, 2010, catalog version 10.5), and all attempted explanations to this huge diversity (Lubin, 1986; Eberhard, 1989; Craig et al., 1994; Köhler and Vollrath, 1995; Opell et al., 2006) have been contentious in one way or another (Lubin, 1986; Craig and Freeman, 1991; Craig and Ebert, 1994; Opell, 1996, 1998; Watanabe, 1999; Zschokke, 2002; Li et al., 2004; Bruce et al., 2005). Based on our findings, we present a new model that could explain the radiation of orbweb spiders.

2. Methods

2.1. Species

We chose *Zosis geniculata* (Olivier, 1789; Uloboridae) and *Metazygia rogenhoferi* (Keyserling, 1878; Araneidae) as representatives of the cribellate and ecribellate orb weavers, respectively. The choice was based on several criteria that enhance comparability between these species. For example, they have a similar adult body size and overall shape, they spin similar-sized orb webs (Fig. 1), both species do not show univoltine life cycle and their families are at the base of the sister clades Deinopoidea (cribellate) and Araneoidea (ecribellate), thus minimizing the effects of these characteristics on the variables being analyzed. Furthermore, in order to control for sexual dimorphism and ontogeny we analyzed only adult females.

We analyzed ten individuals of *M. rogenhoferi* and twenty individuals of *Z. geniculata*. Specimens from both species were collected in the city of São Paulo. Adult females were brought to the lab and kept inside individual acrylic boxes (31 cm × 31 cm × 12 cm) in a room with a 12:12 light cycle and small temperature (24–26 °C) and humidity (76–81% UR) variation. Many *M. rogenhoferi* specimens died in the first week at the laboratory due to nematoid or fungus parasitism. After this first week
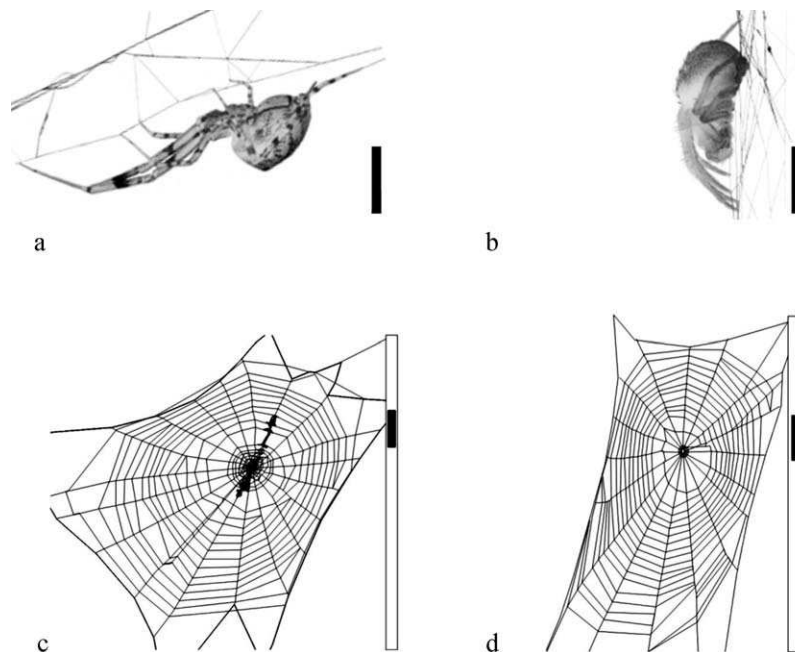

Fig. 1. *Zosis geniculata* (a) and *Metazygia rogenhoferi* (b), scale 3 mm. Drawings based on photographs of webs of *Z. geniculata* (c) and *M. rogenhoferi* (d), scale 2 cm.

precaution period (to exclude parasitized individuals), spiders were not fed for at least three days prior to measurement of oxygen consumption. All spiders were weighted before respirometric measurements. The weight was used to model the allometric parameter in the statistical analysis.

2.2. Respirometry

We used a flow-through intermittent setup. Spiders were inserted into a cylinder shaped test chamber (80 mL) plugged at both ends with three-way valves and partially covered with humidified filter paper to maintain air humidity and to allow the spiders to acquire resting posture. The chambers with spiders were maintained at 25 °C of temperature along all the measurement. The spiders were initially given 1 h to achieve rest condition. After this first hour, the chamber was purged with outdoor air and then left closed for 4 h. After this period, the air was drawn from the chambers for 4 min, and passed through carbon dioxide and water absorbers before going into the PA-1 oxygen analyzer (Sable Systems Inc.). The air flow used was 150 mL/min and did not seem to disturb spiders. Oxygen depletion between the initial and final sampling was estimated via integration (DatacanV software from Sable Systems Inc.) and used to calculate metabolic rates over the time interval.

The resting metabolism was measured in the lightened period of the day, which is the period of lowest activity for spiders. The oxygen consumption of each animal was recorded three times and only the lowest value for each spider was considered. Spurious values (e.g. values from the same day consistently above the others) were discarded. In order to avoid hypoxia effects we estimated the initial condition of oxygen volume in the chamber based on a concentration of 21% of atmospheric air. The oxygen depletion during 4 h of experimentation was quite low (higher value around 0.01%) for both spider species, ensuring that there were no hypoxia effects. Carbonic gas production was even lower if we consider a respiratory quotient of around 0.7 (Lighton et al., 2001) making hypercapnia effects unlikely. For this reason, we are confident that there were no physiological changes due to changes in the gas composition inside the chambers during the 4 h of measurement. All consumption values were corrected to S.T.P. conditions, allowing comparison to literature values. The raw respirometric measurements and body masses of the analyzed individuals can be found in online Supplementary Data.

2.3. Statistical analysis

The relationships between metabolic rates (MR) and body mass (BM) were modeled as MR = aBM^b, which can be modeled linearly in its logarithmic form: $\ln(MR) = \ln(a) + b \times \ln(BM) + \varepsilon$, with $\ln(a)$ as the intercept, b as the slope and ε as the error. The different hypotheses of allometry were investigated through a likelihood-based model-selection approach assuming a normal distribution for the error term ε. Even though we evaluated different species we did not model phylogenetic dependence of the error term, given that allometric relationships between MR and BM are usually understood as products of physical characteristics of the system (Chaui-Berlinck, 2006; Silva et al., 2007; Glazier, 2009).

To compare the measurements obtained for both species with the theoretical model proposed by Lighton et al. (2001) for land-arthropods (excluding ticks and scorpions), we modeled the slope and intercept for each species according to six proposed models. The null model (model 0) evaluates if the allometric curves of both species can be modeled with the equation for land-arthropods. Model 1 uses only one allometric curve for the whole sample (for the two species) but estimates all parameters. Model 2 sets two allometric curves, one for each species, with all parameters being

Table 1
Summary of the tested models. See Section 2 for further description.

	Description
Model 0	Parameters from Lighton et al. (2001); error estimated
Model 1	Parameters estimated for the full sample; different errors
Model 2	Parameters estimated for each species individually; different errors
Model 3	Intercept estimated for each species; same slope; different errors
Model 4	Intercept estimated for each species, same slope and error
Model 5	Intercept estimated for *Metazygia rogenhoferi*; *Zosis geniculata* modeled as Lighton et al. (2001)

estimated independently for both. As some of the estimated parameters had overlapping confidence intervals (see Section 3, Table 2), we constructed reduced versions of the two-allometries model, with parameters being estimated jointly for both species. Thus, model 3 uses the same slope for both allometries, and model 4 uses the same error and slope for both allometries. Model 5 models *Z. geniculata* as a land-arthropod, following Lighton et al. (2001), and *M. rogenhoferi* as having the same slope as *Z. geniculata*, but different intercept. These models are summarized in Table 1, and their justifications will be further explained below. In this way, we evaluated: (1) if both species present the same or distinct allometric relationships; (2) if the parameters of those relationships are the same or different among species; (3) if they conform to the predictions given by the interspecific allometry estimated for land-arthropods.

The parameters were estimated through maximum likelihood optimization. As different models differ in the number of parameters, we extracted the second order Akaike Information Criterion (AIC$_c$; Akaike, 1974), which not only penalizes the likelihood of a given model as a function of the number of parameters, but also corrects for low sample size. AIC$_c$ is calculated as: $AIC_c = -2 \log L + 2K + 2K(K + 1)/(n - K - 1)$, with L being the likelihood of a given model, K the number of parameters in the analysis and n the sample size. AIC$_c$ gives a general measure of fit between the model and the data, and in order to compare two competing models we first rescaled the likelihood for each model as follows: $L' \sim \exp[(-1/2)\Delta AIC_c]$, with ΔAIC_c being the difference between the estimated AIC$_c$ of a given model and the lowest AIC$_c$ in the analysis. To select between two competing models we employed a likelihood-ratio test. The ratio between two rescaled likelihoods is an overall account of the strength of the observed evidence in favor of a given model in relation to another, favoring most parsimonious explanations. Ratios superior to 8 were taken as strong evidence in support of one hypothesis over the alternative one (Royall, 1997). The tests were performed in the order that they were presented above, from less complex (model 0) to more complex (model 2) and then selectively reducing spurious parameters (models 3–5), always with models with more parameters in the numerator. This way we test for the existence of evidence in favor of models with more parameters, rejecting more complex ones when ratios are inferior to the cut-off value ($L' < 8$). The preferred model (less complex or the one favored by the test) in one step was then tested against the following model in the next test. All the statistical analyses were run in R software, version 2.10.0 (R Development Core Team, 2010).

3. Results

M. rogenhoferi (Araneidae) shows on average a higher resting metabolism than *Z. geniculata* (Uloboridae), despite the fact that it also shows smaller body mass. The estimated parameters for the various models are summarized in Table 2. The statistics are depicted in Table 3. From model 0 to model 2, the addition of new

Table 2

Parameters of the models estimated by maximum-likelihood optimization. Each value is presented with the confidence intervals (in parentheses). The left values in models 2–4 are the estimated parameters for *Metazygia rogenhoferi* and the right ones the parameters estimated for *Zosis geniculata*. NA indicates the values obtained from Lighton et al. (2001) model for land-arthropods.

| Model	$\ln(a)$ (intercept)		b (slope)		ε (error)	
0	NA		NA		0.452 (0.358/0.596)	
1	−3.535 (−4.536/−2.534)		0.292 (0.056/0.529)		0.303 (0.240/0.399)	
2	−0.905 (−1.916/−0.207)	−1.296 (−2.384/−0.208)	0.889 (0.484/1.236)	0.985 (0.665/1.304)	0.149 (0.102/0.249)	0.206 (0.155/0.291)
3	−0.623 (−1.716/0.464)	−1.386 (−2.304/−0.473)	0.958 (0.754/1.166)		0.149 (0.102/0.250)	0.206 (0.155/0.291)
4	−0.581 (−1.653/0.491)	−1.351 (−2.161/−0.540)	0.969 (0.798/1.112)		0.189 (0.150/0.249)	
5	−1.037 (−1.159/−0.914)	NA	NA		0.192 (0.152/0.253)	

Table 3

Statistics for the fitted models. K is the number of parameters, $-2\log L$ is the negative log-likelihood, AIC_c is the second order Akaike Information Criterion, ΔAIC_c is the difference between the model's AIC_c and the lowest AIC_c found and L' is the rescaled likelihood value.

	K	$-2\log L$	AIC_c	ΔAIC_c	L'
Model 0	1	37.54099381	39.68385096	49.22411325	2.05E − 11
Model 1	3	13.48714467	20.41022159	29.95048389	3.14E − 07
Model 2	6	−16.1895128	−0.53733889	9.002923405	0.01109277
Model 3	5	−16.08339752	−3.583397517	5.956864778	0.05087252
Model 4	4	−14.8292624	−5.229262404	4.310999891	0.11584526
Model 5	2	−13.98470674	−9.540262295	0	1

parameters to be estimated greatly increases the explanatory power of the model, as is evident by the decrease of the negative log likelihood and of the error term. Particularly remarkable is the huge increase in explanatory power from model 1 to 2, showing that, despite the doubling of the number of parameters, the penalized likelihood increases almost ten thousand-fold. The confidence intervals of the parameters in model 2 are, however, overlapping, an indicative that further reduction in the number of parameters is possible. Model 3 presents the same slope for both models, slightly increasing the explanatory power, but still presents overlapping errors and intercepts. Model 4 further improves the explanatory power by introducing a single error term but the confidence intervals of the intercepts are still superposed. A further reduction of this model would result in model 1, with parameters being estimated jointly for both species, a model that is not as well-supported by the observations as model 4 (Table 3). It is noteworthy that, in spite of the overlap between intercepts, the confidence interval for the intercept of *M. rogenhoferi* does not overlap with the same parameter estimated by Lighton et al. (2001), while *Z. geniculata*'s does [$\ln(a) = -1.746$; after the appropriate transformations]. The slope estimated by Lighton et al. (2001) also falls within the range of the one estimated in model 4 ($b = 0.856$; after the appropriate transformations). For these reasons, we built model 5 using Lighton et al.'s estimates for both species, except for the intercept of *M. rogenhoferi*. This model showed high explanatory power, small errors and narrow confidence interval for the estimated parameter.

The likelihood-ratio tests are summarized in Table 4. The test shows that a two-allometries model is better suited to explain the relation between metabolic rate and body mass in these two species, as evident by the ratio between models 1 and 2. The reduction of the number of parameters did not result in any

significant increase (or decrease) in explanatory power, as shown by the tests involving models 3 and 4, but they were always preferred, as they presented fewer parameters. The test between model 4 (the simplest two-allometry model based only on our data) and model 5 (two-allometry model based on literature) shows that there is no evidence to suggest that the estimated parameters for *Z. geniculata* differ from those predicted by Lighton et al. (2001), which models the allometric relation as: MR (mL/h) = 0.174 × BM (mg)^0.856. In fact, there seems to be a significant amount of evidence supporting the last model [likelihood ratio (model 5/model 4) = 8.632]. This implies that, although *Z. geniculata* has the resting metabolism expected for land-arthropods of the same mass, *M. rogenhoferi* shows a distinct allometric relation between body mass and metabolic rate, presenting values superior to those expected for land-arthropods of the same mass (Fig. 2). Hence, the allometric relation for *M. rogenhoferi* can be modeled as: MR (mL/h) = 0.355 × BM (mg)^0.856.
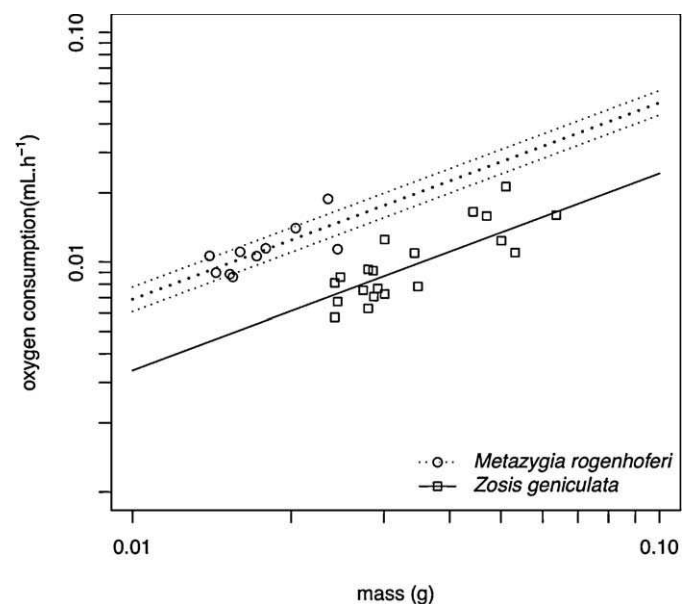
Fig. 2. Graphical representation of the preferred two-allometries model (model 5) showing the relationship between rest metabolic rate measured as oxygen consumption (mL/h) and body mass (g). The axes are logarithmized.

Table 4

Results of the likelihood-ratio test of the fitted models. The preferred model for each test is highlighted in bold.

Test	Likelihood ratio
Model 1/model 0	1.53E + 04
Model 2/model 1	3.54E + 04
Model 2/**model 3**	0.218050343
Model 3/**model 4**	0.439142005
Model 4/**model 5**	0.11584526

4. Discussion

4.1. Resting metabolism of orbweavers

Our analysis unambiguously discards a one-allometry model for both species, pointing the existence of two distinct allometric curves correlating metabolic rate and body mass, with the ecribellate orbweaver presenting a higher metabolism than the cribellate one (Fig. 2). The new two-allometries model contradicts the idea that spiders can be simply understood as land arthropods in energetic terms (Lighton et al., 2001). Previous works have already suggested that tarantulas and spiders from the family Araneidae could be in the lower and upper limits of variation of metabolic rate found among spiders, respectively (Anderson, 1996, 1970; Anderson and Prestwich, 1982; Shillington, 2005). Despite these long known tendencies, no previous work has actually tested the validity of these assumption.

Previous works failed to find any clear resting metabolism differences among different groups of spiders. Greenstone and Bennett (1980) investigated the alleged lower metabolic rate of Scytodidae, which includes brown recluse spiders known to survive almost a year without food, but found no significant difference to other spiders. Anderson (1994) presented a comparative analysis using species from the Theridiidae family with distinct life styles but only found an effect of low metabolism apparently caused by food restriction. It is also possible that the differences in the life style aspects explored by these authors had only a slight energy impact in these spiders' energetic budget and could simply be the result of changes in energy use from one activity to another, through changes in behavior with similar costs. This is a plausible mechanism that could allow the resting metabolism to remain working in the same level despite apparent drastic changes in ecology.

On the other hand, Shillington (2005) found a higher rest metabolism in males, behaviorally more active than female of the same tarantula species, suggesting that sexual differences in tarantulas habits could affect intraspecific difference in metabolic rate. These results also suggest the necessity to inspect the behaviors from the energetic point of view in a more useful way to elucidate the metabolic rates rules. Our work presents the first comparative measurement of cribellate and ecribellate orb weavers, also showing the first evidence that the presence of the cribellum has an impact on the energetic metabolism of spiders, probably due to the overall change in behavior and pattern of activity relative to web building activities.

A higher metabolic rate would demand an enhanced foraging effort by the organism in order to fulfill the elevated energetic needs, a factor that is usually associated with a higher predation risk (Angilletta et al., 2003). In this manner, the connection between a higher metabolic rate and an increase in species richness is not straightforward, but it is exactly what is found in Araneidae. Below we will briefly expose a model that could explain such complex association.

4.2. An alternative model for Araneoidea diversification

Since the resting metabolic rate is coupled to activity metabolic rate (Bennett, 1991; Reinhold, 1999; Hulbert and Else, 2000; Shillington, 2005), the higher resting metabolism of ecribellate spiders, such as M. rogenhoferi, could also be correlated to a higher activity metabolism, allowing a more active and exploratory behavior. This is indeed what happens with our model organisms, as M. rogenhoferi is more prone to activity than a cribellate orbweaver, reconstructing webs and changing web sites more frequently than Z. geniculata (Kawamoto and Japyassú, 2008). The increase of energetic costs in one behavioral function could be

obtained by the allocation of energetic savings from other functions, in an evolutionary process known as allocation trade-off (Angilletta et al., 2003). The evolution of a cheaper web-building and web maintenance in viscid orbweavers would have paved the way for increased metabolic rates, which in turn allowed higher levels of activity. If the generalist microhabitat choice of the orbweavers of the family Uloboridae (Eberhard, 1971) was prevailing when these spiders traded-off a cheaper web for a costly metabolism, the increased activity pattern of the emerging clade (viscid orbweavers) could result in the exploration of a variety of niches derived from the evolution of winged insects (Vollrath and Selden, 2007), thus explaining the radiation of Araneoidea. In this way, the cheaper web would be a step to the key feature that allowed species diversification: the expensive and enhanced mobility of ecribellate orbweavers.

The association between the loss of the cribellum and the evolution of a more diversified clade could be a more general phenomenon. The cribellum has been lost multiple times along the spider phylogeny (Lehtinen, 1967) and many cribellate groups are sister to more diverse ecribellate clades (Kawamoto, 2007; Kawamoto and Japyassú, 2007; Spagna and Gillespie, 2008; Blackledge et al., 2009). Behavioral evidence suggests that the loss of the cribellum is related to an increased pattern of activity (Forster, 1970; Kawamoto, 2007; Kawamoto and Japyassú, 2007), indicating that any model that tries to explain the high diversity of ecribellate orbweavers could possibly be an instance of a more general model of spider biodiversity.

5. Conclusion

Our two species study has reinforced the idea that Araneidae has higher resting metabolism compared to the general expectations for land arthropods. This high metabolism is associated to an important evolutionary web type transition which is frequently cited as the cause of orbweb radiation. We put forward a model that could explain, from a physiological standpoint, the possible correlation between energetic budget and species diversity in spiders. Variation in such basic physiological parameters certainly has strong fitness consequences, and we expect that our findings motivate the exploration of the possible evolutionary outcomes of changes in the metabolic rate of spiders.

Acknowledgments

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.jinsphys.2011.01.001.

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