



Effects of diet and water supply on energy intake and water loss in a mygalomorph spider in a fluctuating environment of the central Andes

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ABSTRACT

The metabolic and water evaporation strategies in spiders may be part of a set of physiological adaptations to tolerate low or unpredictable food availability, buffering spiders against environmental fluctuations such as those of the high mountains of the central Andes.

The aim of this study is to analyze experimentally the variations in metabolic rate and the rate of evaporative water with food and/or water restriction in a high mountain mygalomorph spider population (*Paraphysa* sp.).

We found that the low metabolism of this spider was not affected by water restriction, but its metabolism was depressed after 3 weeks of food deprivation. The spider did not show seasonal metabolic changes but it presented seasonal changes in the rate of evaporative water loss at high temperatures.

Females with egg sacs reduced their metabolic rate and evaporative water at high temperatures.

These findings constitute a set of possible adaptations to a highly fluctuating Mediterranean environment, which is completely covered with snow for many months and then progresses rapidly to a very dry climate with high temperatures.

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1. Introduction

The metabolic rate of spiders is about half that reported in other ectoderms of similar mass (Anderson, 1970, 1974; Carrel and Heathcote, 1976; Angersbach, 1978; Greenstone and Bennett, 1980; Anderson and Prestwich, 1982, 1985; Paul et al., 1987; Strazny and Perry, 1984; Schmitz and Perry, 2001; Canals et al., 2008), which has been considered as an energetic adaptation to their predation strategy. This has led to many studies trying to relate predator type to metabolic rate (Carrel and Heathcote, 1976; Angersbach, 1978; Greenstone, 1978; Greenstone and Bennett, 1980; Paul et al., 1987; Strazny and Perry, 1984; Schmitz and Perry, 2001), and to the proposal that the low energy consumption of spiders is a strategy of “sit and wait” predators in a similar way to that found in ticks (Lighton and Fielden, 1995) and in the antlion *Myrmeleon hyalinus* (Scharf et al., 2009). It has also been proposed that metabolic performance would be enhanced by the ability to depress metabolic rates under usual resting levels during transient periods of food deprivation (Ito, 1964; Miyashita, 1969; Nakamura, 1972; Anderson, 1974; Humphreys, 1977). Canals et al. (2008) found that the mygalomorph

spider *Grammostola rosea* showed very low oxygen consumption at rest, requiring a partial pressure difference of only 0.12–0.16 kPa oxygen between the external and internal environment to meet their oxygen demand. However, they also found that metabolic rate was reduced by food deprivation after 2 weeks, but only at higher temperatures (30 °C in this study), suggesting that metabolic depression is apparent with the high requirements imposed by the temperature–metabolism relationship. Because high metabolic rates are related to high rates of water exchange and evaporation, it is also possible that metabolic depression is a mechanism to avoid water loss through evaporation.

In mygalomorph spiders the rate of water evaporated (mg/cm² h) significantly increases at 40 °C, which means that fluctuating environments with high temperatures, can be very stressful for these spiders (Figueroa et al., 2010). Desiccation is a significant stress for terrestrial arthropods and several mechanisms to achieve desiccation resistance have been noted: (i) reducing the rate of water loss, (ii) increasing the bulk amount of water available to lose and (iii) increasing the tolerance to water loss (Gibbs et al., 1997; Bazinet et al., 2010). For example, in insects, respiratory water loss may be reduced by controlling respiratory patterns (Chown, 2002; White et al., 2007), and cuticular water loss can be controlled by variations in the permeability or epicuticular hydrocarbons (Gibbs, 2002). Also bulk water can be increased by increasing hemolymph volume (Hadley, 1994) or by accumulating

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glycogen (Gibbs, 2002). The mechanisms determining water loss tolerance are not well understood, although trehalose and heat shock proteins have been implicated in cellular protection of organism that survive losing large quantities of water (Watanabe, 2006; Benoit et al., 2010). Also photoperiodic diapauses can increase desiccation resistance. For example, in *Aedes albopictus* diapause eggs had one-third more surface hydrocarbons and one-half the water loss rates of non-diapause eggs (Urbanski et al., 2010).

Some studies have focused on the relationship between evaporation and the environment living species of spiders (Vollmer and Mac Mahon, 1974; Edney, 1977; Hadley et al., 1981; Hadley and Quinlan, 1989). Thus for example Hadley et al. (1981) showed that lycosid species from xeric environments have lower evaporation rates than species that live in caves, and Hadley and Quinlan (1989) suggested that the low rate of evaporation of the black widow spider *Latrodectus hesperus* allowed it to invade successfully the southwestern desert habitats in North America.

The metabolic and water evaporation strategies in spiders may be part of a set of physiological adaptations to tolerate low or unpredictable food availability (Mc Nab, 2002) buffering spiders against environmental fluctuations such as those of Mediterranean climates (Canals et al., 2008). The high mountains of the central Andes, where there are large fluctuations in temperature and humidity and where snow covers large areas for much of the year, conditioning the availability of prey, is a stressful environment for mygalomorph spiders that live and breed there, and should affect their physiological machinery. Mountain spiders may manifest metabolic depression from food deprivation as a way of saving energy (Ito, 1964; Miyashita, 1969; Nakamura, 1972; Anderson, 1974; Humphreys, 1977; Canals et al., 2008) or manifest differences in the rate of water evaporation associated with different environmental conditions (Vollmer and Mac Mahon, 1974; Edney, 1977; Hadley et al., 1981; Hadley and Quinlan, 1989; Figueroa et al., 2010).

The aim of this study is to investigate experimentally the variations in metabolic rate and the rate of evaporative water with food and/or water deprivation in a high mountain mygalomorph spider population.

2. Materials and methods

2.1. Animal model and study area

Sampling was conducted in the mountainous area of Farellones (2200 m) in an area dominated by low shrubs, principally *Chuquiraga oppositifolia*, *Ephedra chilensis*, *Acaena andina* and *A. splendens* (Rosaceae). This area is covered by snow most of the year, from autumn to mid-spring, and may vary from year to year. The temperature in the warm season varies from 20 to 50 °C in the soil, but can reach 50 °C in rocks exposed to the sun. The terrestrial fauna is composed of small rodents, lizards, insects such as ants and phasmids and arachnids, which during the cold season live under snow cover.

A resident population of a single species *Paraphysa* sp., characteristic of this area, was used as a study model (Figueroa et al., 2010; Veloso et al., in press). This is a mygalomorph spider with body mass ranging between 6 and 10 g which inhabits the central mountains above 2000 m. It is a crepuscular and nocturnal spider, although males of this species occasionally can be seen at noon. During the day it can be found in shelters under flat stones and in the cold season it is inactive. Its reproductive period occurs between December and January.

2.2. Sample and experimental design

During the austral spring and summer of 2009 and 2010, 64 adult females of this species were carefully captured using manual

removal of rocks to avoid cuticular damage, and the spiders were immediately taken to the ecophysiology laboratory of the Faculty of Sciences of the University of Chile in Santiago. The first capture period (Dry sample) was conducted during the Dry season in mid-December 2009 (early summer) and the second capture period (Wet sample) immediately after the snow melted, which in 2010 happened during the first days of November (Spring).

In the laboratory, animals were kept separate in transparent boxes of 34 × 34 × 7 cm at 20 °C ± 4 °C and photoperiod of 12 h:12 h L:D. Twenty-eight individuals were used from each sample: Dry ($m_b = 5.38 \pm 2.23$, average ± standard deviation) and Wet ($m_b = 5.79 \pm 1.64$). Each sample was randomly divided into four groups of seven individuals each and assigned to one of the following treatments: (Group 1) water and food *ad libitum* (W+F+); water was administered by maintaining a moist cotton ball in the bottom of the box and the spiders were offered 2–3 larvae of *Tenebrio molitor* daily as a food source (total mass = 0.2402 ± 0.031 g); (Group 2) without water, food *ad libitum* (W–F+); (Group 3) water *ad libitum*, without food (W+F–); (Group 4) without water or food (W–F–). The spiders were kept in these conditions for 3 weeks and then were subjected to the experimental trials. If an individual moulted it was replaced by another individual that was subjected to identical experimental conditions. Females that spun an egg sac were maintained in the experimental conditions, but during measurements the egg sac was removed.

2.3. Evaporative water loss and CO₂ production at different temperatures

After the period of conditioning, total evaporative water loss (TEWL) and CO₂ production (V_{CO_2}) were measured at temperatures of 30°, 35° and 40 °C because the preferred temperature of this species is near 30, and 40 °C is near the critical maximum temperature (Figueroa et al., 2010; Veloso et al., in press). The animals were weighed using an electronic balance SHIMADZU AUX 220 (±0.01 g) and then placed in metabolic chambers of 100 cc specially designed for the metabolic trial. All metabolic measurements were made during the day, which corresponds to the resting phase of this species, with the metabolic chamber in the dark. Only one trial (at one temperature) was performed each day. The animals were separated at 6:00 h and measurements began at 14:00 h, ensuring a fast of at least 6 h. We used a computerized open flow system for determination of CO₂ production (Sable Systems). The equipment was calibrated at the factory for CO₂ and in the lab for O₂ with a known mixture of oxygen (20%) and nitrogen (80%) which was certified by chromatography (BOC, Chile). The metabolic chamber received dried air at a flow of 50 ml/min. The air passed through columns of Drierite and Baralime to remove water and CO₂, respectively. We recorded the total evaporative water loss with a hygrometer attached to the metabolic chambers (Sable Systems). The outputs of the water and CO₂ analyzers were digitized using a Universal Interface II (Sable Systems) and recorded on a personal computer using EXPEDATA data acquisition software (Sable Systems). Our sampling interval was 1 s. The spiders were kept in chambers for at least 3 h during each metabolic trial, and measurements were taken when the records were stabilized, approximately 30 min after the beginning of the trial.

2.4. Analyses

To rule out effects of body size on the analyzed variables, the body mass of the different groups in the sample periods was analyzed with a two way ANOVA. To analyze the experimental effects on V_{CO_2} , a repeated-measures factorial ANOVA was performed, using as factors the sample period (Wet and Dry), diet (W+F+, W+F–, W–F+ and W–F–) and temperature (repeated measure:

30, 35 and 40 °C). Females with egg sacs were excluded. Tukey multiple comparisons and one tailed planned comparisons were performed. Previous to these analyses, normality and homoscedasticity assumptions were tested. Later, a second analysis was performed using the reproductive variable (ES). This was an ANOVA including the egg sac factor (ES+ and ES–), but without considering the diet factor because of mixed numbers and because only a few females in each group had egg sacs.

3. Results

Initial body mass was similar in all experimental groups ($F_{3,48} = 0.165$, $p = 0.91$) and in both capture periods ($F_{1,48} = 0.557$, $p = 0.46$).

3.1. Carbon dioxide production

We did not find a global effect of the capture period on V_{CO_2} ($F_{1,38} = 0.315$, $p = 0.58$), but there were clear V_{CO_2} differences attributable to diet ($F_{3,38} = 3.95$, $p = 0.015$) and to temperature ($F_{2,76} = 269.3$, $p \ll 0.001$) without interaction among these variables ($F_{6,76} = 0.89$, $p = 0.51$) (Fig. 1). Multiple comparisons showed that carbon dioxide production was different at the three different temperatures (Table 1). However the diet effect was uneven in the Dry and Wet periods ($F_{3,38} = 3.08$, $p = 0.038$ for diet–sample period interaction). Multiple comparisons showed that independent of the water supply, diets with food had greater V_{CO_2} than those without food and that effect was more evident in the spiders captured in the Dry period. In the planned comparisons we obtained: (i) water effects: we did not find differences caused by water suppression with or without food (W+F+ vs. W–F+, $t = 1.03$, $p = 0.15$ and W+F– vs. W–F–, $t = 1.4$, $p = 0.09$), (ii) food effects: with and without water, a decrease in V_{CO_2} caused by food deprivation was found (W+F+ vs. W+F–: $t = 2.21$, $p = 0.015$ and W–F+ vs. W–F–: $t = 1.75$, $p = 0.045$).

Female spiders with egg sac ($n = 11$; 5 in the Dry sample and 6 in the Wet sample) showed lower V_{CO_2} ($F_{1,52} = 5.12$, $p = 0.027$). In the same analysis the effect of temperature was confirmed (now for all individuals, with and without egg sac) ($F_{2,104} = 194.24$, $p \ll 0.001$) as well as the lack of sample period effect on V_{CO_2} ($F_{1,52} = 0.43$, $p = 0.52$) and the lack of variable interactions ($p > 0.05$) (Table 2 and Fig. 2).

3.2. Evaporative water loss

There was an increase in evaporative water loss with increase of temperature ($F_{2,76} = 178.8$, $p \ll 0.001$). There was also a difference in water loss between capture periods ($F_{1,38} = 5.7$, $p = 0.022$) which was only significant at 40 °C, without differences attributable to the diet factor ($F_{3,38} = 2.23$, $p = 0.10$). A positive interaction between capture period and temperature was found ($F_{2,76} = 6.20$, $p = 0.003$); water loss was greater during the Wet capture period, but again this was only evident at 40 °C (Table 3 and Fig. 3). Analyzing exclusively water loss data at 40 °C, the capture period effect on water loss was confirmed ($F_{1,39} = 3.90$, $p = 0.05$), but diet effects ($F_{3,39} = 1.1$; $p = 0.35$) and interaction effects on water loss were not found ($F_{3,39} = 2.4$, $p = 0.08$). The total water loss during the time of the trials (2.5 h) at 40 °C was 68.97 mg (1.28% of the initial body weight (m_{bi})) in the Dry sample and 103.10 mg (1.78% m_{bi}) which means that these spiders could loss 12.3% m_{bi} and 17.2% m_{bi} , respectively, probably reaching their maximal limit of desiccation tolerance (Vollmer and Mac Mahon, 1974).

Comparing the evaporative water loss between females with and without egg sacs, the greater water loss at 40 °C ($F_{2,104} = 83.26$, $p \ll 0.001$) and the increase of water loss in the Wet capture period was confirmed ($F_{1,52} = 6.90$, $p = 0.011$), with a marginal decrease of evaporative water loss in females with egg sacs ($F_{1,52} = 3.28$, $p = 0.07$) which is evident in the temperature–egg sac interaction ($F_{2,104} = 4.11$, $p = 0.02$) (Fig. 4). Multiple comparisons revealed that these differences only occurred at 40 °C (Table 4). When we analyzed only data at 40 °C we found the same

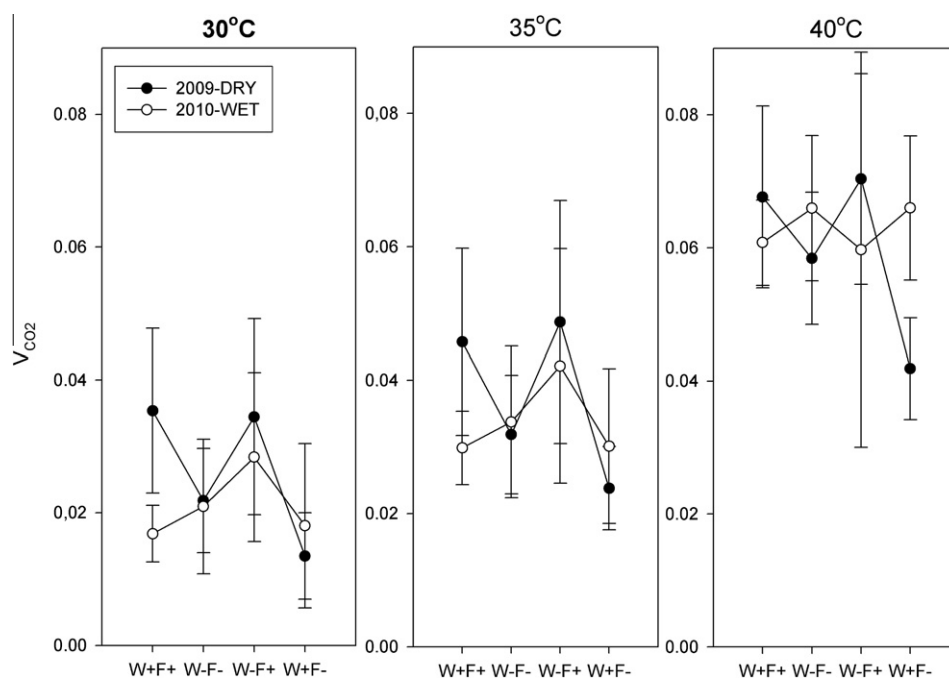


Fig. 1. Carbon dioxide production (mlCO_2/gh) at three temperatures in *Paraphysa* sp. captured in two periods (Dry and Wet) and with four different diets (see text).

Table 1
Carbon dioxide production ($\mu\text{CO}_2/\text{gh}$) at three temperatures in *Paraphysa* sp. captured in two periods (Dry and Wet) and with four different diets (see text). Different letters indicate significant differences ($p < 0.05$) in Tukey multiple comparisons.

	30 °C		35 °C		40 °C	
	Dry	Wet	Dry	Wet	Dry	Wet
W+F+ ab	35.4 ± 12.4	19.9 ± 4.3	45.7 ± 14.0	29.8 ± 5.5	67.6 ± 13.7	60.8 ± 6.4
W-F- b	21.8 ± 7.9	20.9 ± 10.1	31.8 ± 8.9	33.8 ± 11.4	58.4 ± 9.9	65.9 ± 10.9
W-F+ a	34.5 ± 14.5	28.4 ± 12.7	48.7 ± 18.2	42.1 ± 17.6	70.4 ± 15.8	59.7 ± 29.7
W+F- c	13.5 ± 6.5	18.0 ± 12.4	23.8 ± 6.2	30.1 ± 11.6	41.8 ± 7.6	66.0 ± 10.8

Table 2
Carbon dioxide production ($\mu\text{CO}_2/\text{gh}$) at three temperatures in *Paraphysa* sp. females with (ES+) and without (ES-) egg sac captured in two periods (Dry and Wet).

	DRY		WET	
	ES-	ES+	ES-	ES+
30 °C	26.1 ± 14.2	15.1 ± 2.3	21.2 ± 10.9	17.8 ± 3.9
35 °C	37.4 ± 16.1	21.9 ± 1.7	33.8 ± 12.9	25.3 ± 7.6
40 °C	58.9 ± 16.7	43.4 ± 4.9	63.2 ± 16.4	58.5 ± 1.7

results for the capture period effect ($F_{1,51} = 7.32, p = 0.009$) and the egg sac effect ($F_{1,51} = 3.65, p = 0.06$).

4. Discussion

The sampling area of the central Andes has a long season in which snow covers the whole area. After the snow melts in the spring, the weather changes to a high altitude dry climate. Under these conditions the *Paraphysa* sp. population lives, captures prey, mates and breeds. The temperature of the rocks in some areas may exceed 50 °C in the dry season, while in winter the temperature in their shelters is less than 0 °C (Veloso et al., in press). In our experiments we compared the response of spiders captured in the dry season (Dry) with others captured when the snow had recently melted. Our results show a spider with a low metabolism, which, calculating the expected oxygen consumption as $\log V_{O_2} = -0.133 + 0.71 \log(m_b)$ with V_{O_2} in $\mu\text{l/h}$ and m_b in mg (Green-

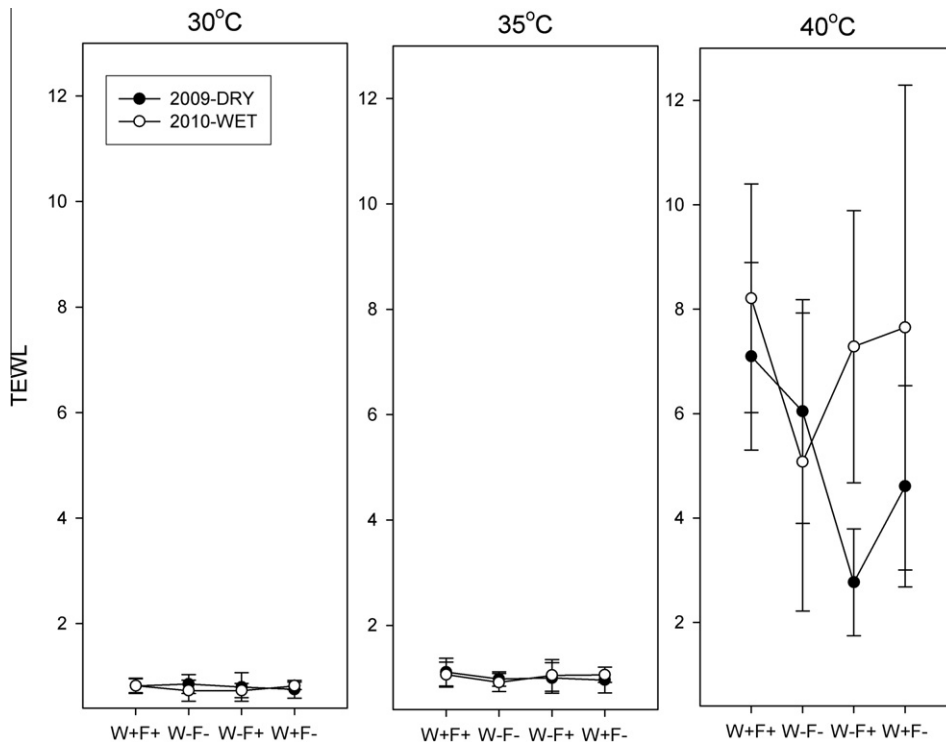


Fig. 2. Carbon dioxide production (mlCO_2/gh) at three temperatures in *Paraphysa* sp. females with (ES+) and without (ES-) egg sac captured in two periods (Dry and Wet).

Table 3
Evaporative water loss at three temperatures in *Paraphysa* sp. (mgH₂O/gh), captured in two periods (Dry and Wet) and with four different diets (see text).

	30 °C		35 °C		40 °C	
	Dry	Wet	Dry	Wet	Dry	Wet
W+F+	0.82 ± 0.14	0.83 ± 0.13	1.11 ± 0.26	1.06 ± 0.24	7.10 ± 1.80	8.20 ± 2.19
W-F-	0.85 ± 0.18	0.73 ± 0.20	0.98 ± 0.14	0.92 ± 0.17	6.04 ± 2.14	5.07 ± 2.85
W-F+	0.79 ± 0.27	0.73 ± 0.14	0.99 ± 0.29	1.05 ± 0.30	2.76 ± 1.02	7.28 ± 2.60
W+F-	0.75 ± 0.17	0.82 ± 0.07	0.96 ± 0.24	1.06 ± 0.14	4.61 ± 1.93	7.64 ± 4.64

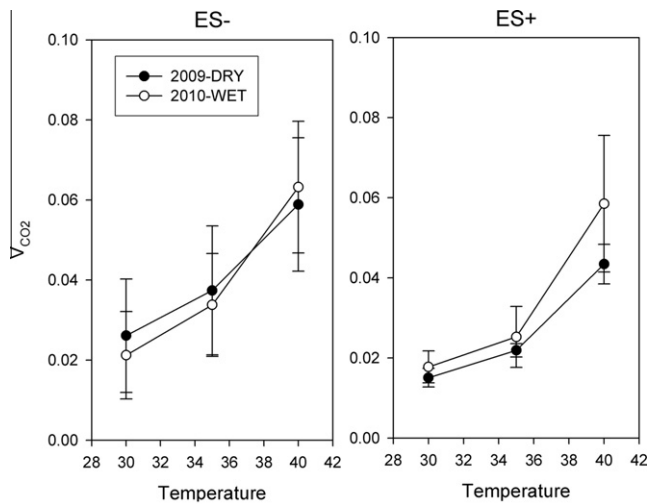


Fig. 3. Evaporative water loss at three temperatures in *Paraphysa* sp. (mgH₂O/gh) captured in two periods (Dry and Wet) and with four different diets (see text).

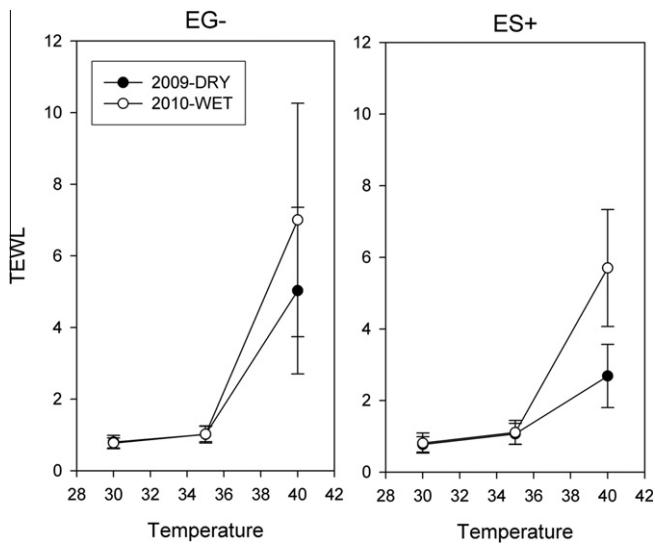


Fig. 4. Evaporative water loss at three temperatures in *Paraphysa* sp. females (mgH₂O/gh) with (ES+) and without (ES-) egg sac captured in two periods (Dry and Wet).

Table 4

Evaporative water loss at three temperatures in *Paraphysa* sp. females (mgH₂O/gh) with (ES+) and without (ES-) egg sac captured in two periods (Dry and Wet). Different letters indicate significant differences ($p < 0.05$) in Tukey multiple comparisons.

	Dry		Wet	
	ES-	ES+	ES-	ES+
30 °C	0.80 ± 0.19 a	0.77 ± 0.21 a	0.77 ± 0.14 a	0.81 ± 0.28 a
35 °C	±0.24 b	1.07 ± 0.29 b	±0.22 b	1.11 ± 0.24 b
40 °C	5.03 ± 2.33 c	2.69 ± 0.88 d	7.00 ± 3.26 e	5.70 ± 1.63 f

stone and Bennett, 1980), and considering a respiratory quotient of $RQ = 0.92$ (Shillington, 2002), corresponds to a 53.2% expected for spiders, typical for mygalomorph spiders (Canals et al., 2008). Its CO₂ production and evaporative water loss are temperature dependent with a sharp increase in evaporative water loss at 40 °C, which has already been reported for *Paraphysa* sp. (Figueroa et al., 2010; Veloso et al., in press), suggesting that this temperature is probably very close to the maximum critical temperature

for the species. This is also consistent with the abrupt change in permeability attributable to the phase change of cuticle lipids (Gibbs 1998, 2002), although other factors can be implicated in the change of cuticular permeability (see Yoder et al., 2009). The capture period did not affect the metabolism, which is consistent with results obtained in other mygalomorphs such as *Aphonopelma anax* (Stoltey and Shillington, 2009), where no metabolic changes were observed throughout the mating season.

The lack of water in the diet did not affect the metabolism or evaporative water loss, which reveals that these spiders are well adapted to water shortages over the time period considered in this experiment, in which the average change in weight attributable to water loss in the dehydrated groups (W-F- and W-F+) was 3.55%. However, results in araneomorph spiders have been contradictory. For example, in *Argiope trifasciata* dehydration caused a decrease in V_{CO_2} at 15° and 25 °C, while in *A. aurantia* dehydration caused an increase in V_{CO_2} at 25 °C (Markezich, 1993). The absence of food for 3 weeks resulted in a decrease of metabolism, which is consistent with previous findings in different species. For example in *Lycosa pseudoannulata* (Ito, 1964), *Pardosa astrigera* (Miyashita, 1969; Tanaka and Ito, 1982) *Lycosa lenta*, *Filistata hibernalis* (Anderson, 1974) and *Latrodectus hasselti* (Stoltz et al., 2010) a decrease in metabolic rate caused by starvation has been reported. This decline in metabolic rate has been attributed in part to a behavioral change in spiders deprived of food, from an active search for prey to a wait phase. Thus the metabolic change could be attributed to a decrease in activity. This may be particularly adaptive in sit and wait predators (Matsura, 1981; Greenstone and Bennett, 1980; Canals et al., 2008). In mygalomorphs a decrease in metabolism due to food deprivation has also been reported. For example, in *G. rosea* metabolic depression was seen at 30 °C in animals subjected to a short starvation period of 3 weeks (Canals et al., 2008). In contrast, the species studied here showed a decrease in metabolic rate which was similar in amount at different temperatures. Our results show metabolic differences between the groups with and without food, however, the spiders were not monitored over time. Thus we cannot determine whether feeding increased metabolism or whether starvation caused the decline. Interesting in this regard are the results of Phillip and Shillington (2010), who found that the mygalomorph spider *Phormictopus cancerides* fed with a cricket every 5 days increased its metabolism, while individuals fed every 30 days maintained their metabolism. The metabolic increase was attributed to specific dynamic action (SDA) or a physiological response associated with feeding (Phillip and Shillington, 2010). It has also been reported that a mygalomorph spider of central Chile *Euathlus truculentus* has an SDA scope of 6.5 ± 1.1 , with a peak at 45 min, but the metabolic increase can last 8 h (Nespolo et al., 2011). In our experiments with *Paraphysa* sp. animals were separated in the morning and measured in the afternoon. This implies that if there were any effects of SDA they would be minimal. Moreover the values obtained at comparable temperatures in postabsorptive animals of the same species by Figueroa et al. (2010) are very similar to those of our animals with food (W+F+ and W-F+) and much higher than the group without food (W+F- and W-F-). This suggests that *Paraphysa* sp. depresses its metabolism with food deprivation of 3 weeks. Moreover, this effect is greater in the dry capture period, which may be a seasonal adjustment to a less predictable or reduced availability of prey. Spiders captured during the Wet period had a greater evaporative water loss at 40 °C than those captured during the Dry period in which temperatures are higher and humidity low. This may be due to changes in the composition of the cuticle such as the proportion of hydrocarbon compounds and lipids; this has been reported among adult females and young in *Tegenaria atrica* (Trabalon et al., 1996). Temporary changes in trans-cuticle water flow have been reported in other arthropods (Hadley and Quinlan, 1987; Toolson and Hadley,

1987; Hadley et al., 1986), but to the best of our knowledge there are no reports of seasonal changes in cuticle permeability in spiders. These findings constitute a set of possible adaptations to a highly fluctuating Mediterranean environment, which is completely covered with snow for many months and then progresses rapidly to a very dry climate with high temperatures. Fluctuating environments may be linked to changes in prey availability and metabolic changes associated with diet. Adaptation to rapid temperature change probably requires changes in the cuticle to avoid dehydration at temperatures above 40 °C that are common in parts of its habitat, which also forces the spider to search for adequate shelters (Veloso et al., in press). Reproduction also imposes new physiological changes and behavioral needs in this spider. Thus the presence of an egg sac is associated with a decrease in metabolism that may be an adaptation to low food consumption in these conditions. This, associated with a possible decrease in water content, involves the search for cooler shelters (Veloso et al., in press), to avoid dehydration.

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