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Body Condition Helps to Explain Metabolic Rate Variation in Wolf Spiders

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Abstract

1. Metabolism is the fundamental process that powers life. Understanding what drives metabolism is therefore critical to our understanding of the ecology and behavior of organisms in nature.
2. Metabolic rate generally scales with body size according to a power law. However, considerable unexplained variation in metabolic rate remains after accounting for body mass with scaling functions.
3. We measured resting metabolic rates (oxygen consumption) of 227 field-caught wolf spiders. Then, we tested for effects of body mass, species, and body condition on metabolic rate.
4. Metabolic rate scales with body mass to the 0.85 power in these wolf spiders, and there are metabolic rate differences between species. After accounting for these factors, residual variation in metabolic rate is related to spider body condition (abdomen:cephalothorax ratio). Spiders with better body condition consume more oxygen.
5. These results indicate that recent foraging history is an important determinant of metabolic rate, suggesting that although body mass and taxonomic identity are important, other factors can provide helpful insights into metabolic rate variation in ecological communities.

Keywords: Allometry, Condition, Lycosidae, Metabolic rate, Respiration, Wolf spider

Introduction

Metabolic rate describes how quickly energy from the environment can be transformed into useful energy within an organism, making it one of the most fundamental measurements of life (Brown et al., 2004). Metabolism powers all processes within organisms, including growth, maintenance, and reproduction. Because of this, understanding what drives metabolism can help to explain larger processes such as individual development, population dynamics, and food web structures (Kleiber, 1961; West et al., 2001; DeLong & Hanson, 2009; O'Connor et al., 2009; Burton et al., 2011).

Body mass is a key determinant of metabolic rate. Metabolic rate generally scales with body mass according to a power-law function:

$$R = R_0 M^\alpha \quad (1)$$

where R is metabolic rate, R_0 is normalized meta-

bolic rate, M is body mass, and α is a scaling constant. There is long-running controversy over the precise value of α and the mechanisms producing it (West et al., 1999; Brown et al., 2004; Glazier, 2006, 2010; DeLong et al., 2010; Isaac & Carbone, 2010; Burton et al., 2011). Historically, there has been support for an average cross-taxon scaling constant of approximately $3/4$, known as Kleiber's law (Kleiber, 1932), but it is now clear that the scaling exponent α varies widely across taxa (Glazier, 2006; White et al., 2006; DeLong et al., 2010). And although body mass plays an important role in determining metabolic rates, there remains a considerable amount of unexplained variation in metabolic rates, even after accounting for size (Burton et al., 2011).

Because metabolic rate reflects the use of food energy to conduct biological work, the availability of food energy to burn (e.g. recently acquired food and/or stored energy) could play an important role in explaining this variation, at least at the individual level. For example, food deprivation or the presence of competitors can decrease food uptake, leading to reduced metabolic

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rates (Dulloo & Jacquet, 1998; DeLong et al., 2014). Furthermore, feeding and activity levels can influence the body mass scaling of metabolic rate, as different activities have different energy costs (Glazier, 2010; DeLong & Hanley, 2013). Thus, we predict that resource intake and allocation can shed light on how variation in metabolic rates arises after accounting for body mass. Considering species-level differences could account for further variation in metabolic rate, as species and individuals might have different strategies for acquiring and using energy (e.g. hunting techniques, reproduction timing) (Herberstein, 2011), which may be reflected in their metabolism.

Here, we determine whether body condition (reflecting the rate of recent food acquisition) can explain variations in the resting metabolic rates of individual wolf spiders (Lycosidae), using four species across two genera (*Hogna* and *Schizocosa*). Wolf spiders can survive extensive periods without eating and can exhibit large variation in body condition (Anderson, 1974). Coupled with their wide body mass range, wolf spiders are therefore an ideal system for measuring metabolism across a spectrum of body condition and body size combinations. Furthermore, body condition in wolf spiders is simple to measure: we used abdomen width over cephalothorax width. As cephalothorax width is fixed relative to body size within molts and abdomen width reflects the intake of food from recent prey capture, this ratio is an indicator of recent/current fuel supply (Persons et al., 2002). Specifically, we test the hypotheses that: (i) wolf spider metabolic rate scales with body mass; (ii) residual variation in metabolic rate after accounting for body mass varies by species; and (iii) residual variation in metabolic rate is positively related to body condition.

Materials and Methods

In June 2018, we collected wolf spiders from grassy areas and alfalfa fields in and around Cedar Point Biological Station in Ogallala, Nebraska, USA by looking for eyeshine at night using headlamps. Although more than a dozen Lycosidae species are present at Cedar Point, four are especially abundant: *Hogna baltimoriana*, *Schizocosa ocreata*, *Schizocosa mccooki*, and an unidentified *Schizocosa* morphospecies. Thus, we focused on these spiders, excluding any females carrying egg sacs or spiderlings. We collected a

total of 235 individual spiders (43, 24, 119, and 49 for each species, respectively). Spiders remained overnight in 120-ml plastic cups containing a piece of damp paper towel to maintain humidity. The following morning, we photographed each individual against a graph paper background. For each spider, we also recorded species, body mass, and body volume. We estimated volume using a density of c. 0.6 g ml⁻¹ based on trials with recently deceased spiders submerged in water (Rueda & Williamson, 1992; Radtke et al., 2006).

Immediately afterwards, we measured resting oxygen consumption as a proxy for metabolic rate with a Presens SDR respirometer (PreSens Precision Sensing, Regensburg, Germany). For all trials, temperature and pressure were c. 23°C and 973 mbar, respectively. We placed spiders individually into 4-ml SensorVials (PreSens Precision Sensing) using cardstock funnels and tightened the caps securely to prevent gas exchange. Eight spiders were too large (> 400 mg) to fit into the vials, so we excluded these spiders from further analysis for a total of 227 respiration measurements. For every run of five 24 simultaneous measurements, we also included a 'blank' vial that contained only air. Aluminum foil wrapped around the vials created a dark environment for the spiders and ensured accurate readings by eliminating external light. For 1 h, the respirometer recorded oxygen levels (ppm) in each tube every 2 min. We released spiders back into their original collection areas after the experiments.

We discarded respiration data from the first 6 min of each oxygen trace to remove the effects of acclimation and system equilibration. We used ordinary least-squares regression to obtain a slope for the relationship between oxygen concentration and time. We subtracted the slope of the blank's line of fit from that of each spider to calculate overall oxygen consumption in ppm min⁻¹. Two very small spiders (< 50 mg) did not have detectable metabolic rates; we excluded these spiders from further analysis. Due to differences in spider size, we accounted for differing initial volumes of air available to each individual in each vial by subtracting spider volume from vial volume (4 ml). From there, we converted oxygen consumption from ppm min⁻¹ (g l⁻¹ min⁻¹) to g min⁻¹ to obtain an absolute metabolic rate for each spider.

From each spider's photograph, we measured the widest part of both the cephalothorax and the

abdomen using IMAGEJ (Rasband, 1997). Abdomen width divided by cephalothorax width served as a proxy for spider body condition (condition ratio), with high condition ratio indicating high resource intake (Anderson, 1974). Because metabolic rate and mass typically have a power-law relation, we log-transformed the data before fitting several linear models in MATLAB. We tried various linear models with metabolic rate as the dependent variable and some combination of mass, condition ratio, and species as explanatory variables. We also generated models containing all combinations of two-way interactions between mass, species, and condition ratio. Then, we selected the model with the lowest Akaike information criterion value where all terms were significant (either independently or in an interaction) as a final model (Burnham & Anderson, 2004).

Our ratio-based condition index was tightly correlated with an index based on residuals from a carapace width–abdomen width regression ($r = 0.97$, $P < 0.001$). To further confirm that our choice

of metric for condition did not influence our results, we ran the best linear model using residuals from a carapace–abdomen regression instead of condition ratio and found similar results using both approaches. Because both condition indices provide quantitatively similar information (Lyon et al., 2018), we used condition ratio here due to the ease of visualizing body shape via the condition ratio (i.e. a ratio of 1.5 refers to a spider with an abdomen 1.5 times wider than its carapace).

Results

Schizocosa ocreata, *S. mccooki*, *Schizocosa* sp., and *Hogna baltimoriana* weighed 0.06 ± 0.02 , 0.12 ± 0.07 , 0.12 ± 0.6 , and 0.27 ± 0.16 g (mean \pm SD), respectively. Our analysis indicated that a linear model with mass, species, and condition ratio as explanatory variables was supportable with the data (Table 1, model 3). In this model, resting oxygen consumption of wolf spiders increased with body mass to the power of 0.85 ($t = 14.13$, $P < 0.001$, 95% CI: 0.73–0.97; Table 2; Figure 1a).

Table 1. Comparison of linear models for respiration rate.

Model	Δ AIC	AIC	Log-likelihood	Condition	Species	Mass	Interaction
1 Ln(resp) ~ ln(mass) + species + residuals	0	244.51	-115.25	Y	Y	Y	-
2 Ln(resp) ~ ln(mass) + species + ratio + ln(mass) \times ratio	-1.22	245.73	-114.86	N	Y	Y	N
3 Ln(resp) ~ ln(mass) + species + ratio	-1.42	245.93	-115.97	Y	Y	Y	-
4 Ln(resp) ~ ln(mass) + species + ratio + ln(mass) \times species	-3.91	248.42	-114.21	Y	Y	Y	N
5 Ln(resp) ~ ln(mass) + species + ratio + species \times ratio	-5.74	250.25	-115.13	N	N	Y	N
6 Ln(resp) ~ ln(mass) + species	-6.72	251.23	-119.61	-	Y	Y	-
7 Ln(resp) ~ ln(mass) + ratio	-22.03	266.54	-129.27	Y	-	Y	-
8 Ln(resp) ~ ln(mass)	-29.25	273.76	-133.88	-	-	Y	-

'Y' or 'N' indicate whether the term is or is not significant, respectively, and '-' indicates the term is not included in the model. 'Condition' refers to either cephalothorax width over abdomen width (i.e. 'ratio') or residuals from an abdomen–cephalothorax regression (i.e. 'residuals'). Models in bold indicate that all terms are significant. AIC, Akaike information criterion.

Table 2. Preferred model (model 3) describing the effects of species, body mass, and condition ratio on respiration rate

Term	Estimate	SE	tStat	P-value
Intercept	-13.56	0.18	-73.71	<0.001
<i>Schizocosa mccooki</i>	0.43	0.09	4.92	<0.001
<i>Schizocosa</i> sp.	0.34	0.10	3.37	0.001
<i>Schizocosa ocreata</i>	0.24	0.14	1.71	0.088
Ln(mass)	0.85	0.06	14.13	<0.001
Ratio	0.36	0.13	2.72	0.007

Terms in bold are significant.

Compared with a model with only mass, including both condition and mass increased R^2 from

0.52 to 0.54. Spiders with higher condition ratios (reflecting higher resource intake) had higher oxygen consumption ($t = 2.72$, $P = 0.007$; Table 2; Figure 1b). *Hogna baltimoriana* had lower respiration rates than *Schizocosa mccooki* ($t = 4.92$, $P < 0.001$) and *Schizocosa* sp. ($t = 3.37$, $P = 0.001$), but was not different from *S. ocreata* ($t = 1.71$, $P = 0.088$) (Table 2; Figure 1c). There was no difference in metabolic rate between the three *Schizocosa* species [*S. ocreata* and *S. mccooki* ($t = -1.74$, $P = 0.084$), *S. ocreata* and *Schizocosa* sp. ($t = 0.894$, $P = 0.372$), and *S. mccooki* and *Schizocosa* sp. ($t = -1.202$, $P = 0.231$)] (Figure 1c).

Discussion

The metabolic scaling exponent found here (0.85, 95% CI: 0.73–0.97) was not distinguishable from the $3/4$ slope predicted by Kleiber's law. However, our estimate is similar to those found in other spider studies: 0.86 in *Damon annulatipes* (Terblanche et al., 2004), 0.86 in *Zosis geniculata* and *Metazygia rogenhoferi* (Kawamoto et al., 2011), and an overall spider scaling estimate of 0.82 across nine studies (Terblanche et al., 2004). However, some studies have produced lower estimates: Greenstone and Bennett (1980) found a scaling exponent of 0.71. These slight differences could be due to the scale of our data. We compared metabolic rates across individuals rather than across species, accounting for taxonomic differences by including species as a factor in our model rather than obtaining one average metabolic rate for each species; Greenstone and Bennett's (1980) analysis simultaneously tested 20 Araneae species together without accounting for phylogeny or species-level differences beyond body size.

There also was considerable variation in metabolic rates that could not be accounted for by body mass. Incorporating body condition improved the explanatory power of our model. Although there is a correlation between recent foraging success and metabolism, it is unclear how this arises. In the case of predators such as wolf spiders, individuals who take in more prey may have higher metabolic rates resulting from this increased resource intake. Alternatively, individuals with higher metabolic rates may be more adept at capturing prey because they have more energy to expend, and faster-moving predators are more adept at finding and subduing prey (Holling, 1959; Hirt et al., 2017). Thus, individual variation in metabolic rate could be inherent (i.e. a trait with functional consequences), plastic (responding to recent foraging history), or both.

Specific dynamic action (SDA), increased metabolism due to actively digesting food, could also play a role (McCue, 2006). Because the spiders tested here were collected in the field and tested shortly afterwards, it is possible that some of the apparent metabolic rate variation is due to differences in the digestion stage (Overgaard & Wang, 2012). Although no SDA data on the wolf spider species used here are available, Jensen et al. (2010) found an increase in oxygen

consumption in the 3-h period after a meal in the wolf spider *Pardosa prativaga*. Because the spiders used here were held without food overnight (c. 12 h) and were not feeding during the trials, it is unlikely that specific dynamic action was responsible for the observed relationship between metabolic rate and body condition.

Although body condition indices are commonly used, there is some uncertainty as to what they measure. Some studies have shown that starved spiders have reduced lipid, carbohydrate, and even protein stores, while water content remains constant or increases (Stewart & Martin, 1970; Collatz & Mommsen, 1975; Knudsen, 2011). Regardless of what nutrient body condition measures, abdomen width is clearly linked to resource intake. Several studies have shown that spiders lose weight (abdomen mass) when

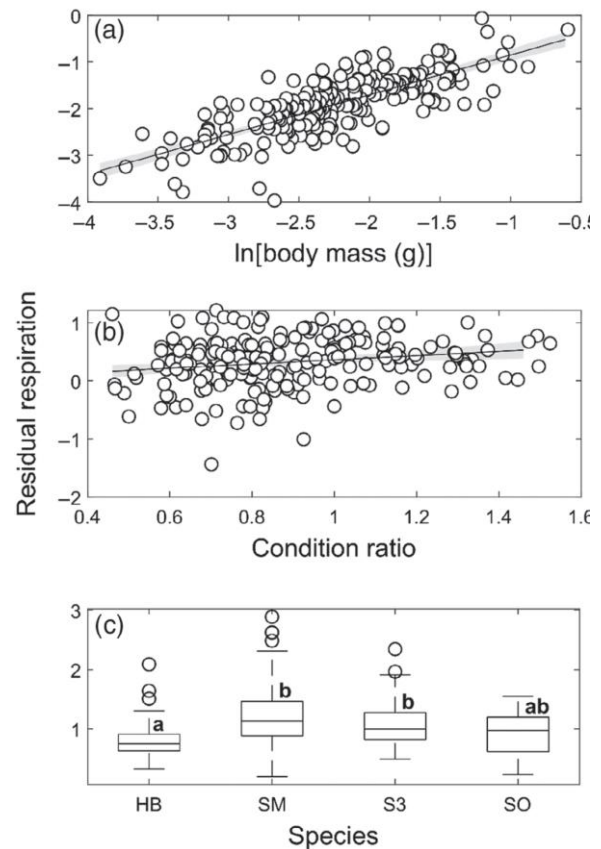


Figure 1. Effects of each term in the preferred linear model (model 3) on respiration rate. (a, b). Partial regression plots of the effect of spider mass (g) (a) and condition ratio (b) on respiration rate (mg O_2 consumed min^{-1}). (c) Respiration rates of *Hogna baltimoriana* (HB), *Schizocosa mccooki* (SM), *Schizocosa* sp. (S3), and *Schizocosa ocreata* (SO) after accounting for mass and condition ratio. Species marked with the same letter are not significantly different.

starved (Nakamura, 1987; Overgaard & Wang, 2012). Furthermore, recent resource intake is undoubtedly important in determining metabolic rates, as spiders' metabolic rates slow under starvation and rapidly recover to pre-starvation levels once food becomes available again (Anderson, 1974; Tanaka & Itô, 1982; Nakamura, 1987).

Thus, prey scarcity may cause a reduction in both body condition and in metabolic rates, leading to the observed correlation between condition and respiration. These physiological adaptations to reduced food availability may increase tolerance of inconsistent prey supplies. The characteristically low metabolic rates of spiders have also been attributed to fluctuating food availability (Anderson, 1970; Greenstone & Bennett, 1980), highlighting the role of prey availability in determining metabolism.

Our results suggest there are taxonomic differences in metabolic rate as well. In general, *Hogna* spiders consumed less oxygen than did *Schizocosa* sp. This may be because *Hogna* are partially subterranean sit-and-wait predators (Dondale & Redner, 1990; Rosenheim et al., 2004) whereas *Schizocosa* mostly hunt above ground, with limited use of burrows (Kaston, 1978; Suttle, 2003). Active hunting may require more energy, which may be reflected in increased metabolic rates for a given body mass (Biro & Stamps, 2010). Of the *Schizocosa* species, *S. mccooki* consumed the greatest amount of oxygen. Although it is unclear why, we postulate that this may be related to differences in reproductive timing. We did not test females carrying egg sacs or spiderlings, but most of those spiders with offspring were *S. mccooki*. Thus, the *S. mccooki* females that did get measured may have been producing (or preparing to produce) offspring, thereby increasing the metabolic rates for individuals of that species.

In explaining metabolic rate variation, we gain insights into other types of variation as well. Mass and metabolic rate are both closely linked to population abundance, foraging rates, and even rates of evolution (Damuth, 1981; Martin & Palumbi, 1993; Ernest et al., 2003; DeLong & Vasseur, 2012). Accounting for variation in metabolic rate might thus help to account for variation in abundance or productivity. A population in better condition may ultimately produce more biomass and more offspring, increasing population sizes above what might be expected for a given

body size. Similarly, understanding metabolic rate variation could also help to explain variation around allometric scaling of predator functional responses (McCann et al., 1998; Rall et al., 2011). Mass, condition, and taxonomic identity all contribute to foraging success (Rall et al., 2012; Kalinoski & DeLong, 2016; Lyon et al., 2018), suggesting that variation in metabolic rate (whether an inherent trait or a response to food intake) may also be important in determining interaction strengths and structuring food webs.

Although our results show how just three factors—body mass, species identity, and body condition—can account for variation in metabolic rate, additional unexplained variation remains. Here, we did not consider sex or age. Although detected differences in body mass and condition may be partially due to these factors, sex and age could account for some of the remaining respiration rate differences between spiders of the same mass, species, and condition (Burton et al., 2011). Nonetheless, our results show that looking beyond mass can provide key insights into metabolism and how it might inform our understanding of individual behavior and development, population dynamics, and ecological communities.

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Author contributions

SFU and JPD designed the project; SFU collected the data; and SFU and JPD analyzed the data and wrote the manuscript.

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