SEXUAL DIMORPHISM IN THE METABOLIC RATE
OF TWO SPECIES OF WOLF SPIDER
(ARANEAE, LYCOSIDAE)

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ABSTRACT.   Spiders have long been noted as classic examples of extreme sexual dimorphism and adaptations to the lifestyle of a sit-and-wait predator. We examined sex-based differences in the metabolic rate of two species of wolf spider that differ in their degree of sexual dimorphism and predatory strategy. *Pardosa milvina* (Hentz 1877) is a small active wolf spider that does not exhibit a large degree of sexual dimorphism in body size. *Hogna helluo* (Walckenaer 1837) is a large, strongly sexually dimorphic wolf spider with large, sedentary females and smaller, active males. We found that *P. milvina* had a higher mass-specific metabolic rate than *H. helluo*. Also, *P. milvina* males had a higher metabolic rate than *P. milvina* females but there was no difference in mass-specific metabolic rate between *H. helluo* males and females. Our data demonstrate that an actively foraging species, *P. milvina*, exhibits a higher metabolic rate than species with a sit-and-wait strategy, *H. helluo*. This suggests that activity levels may be correlated with metabolic rates. In addition, we hypothesize that sexual selection and selection for specific reproductive roles may have resulted in species differences in sexual dimorphism for metabolic rate.

Keywords: Wolf spider, *Pardosa milvina*, *Hogna helluo*, sexual selection, predation

The low metabolic rate of spiders and other arachnids has been suggested as an adaptation to living in environments with unpredictable food supplies (Anderson 1970; Greenstone & Bennett 1980; Anderson & Prestwich 1982; Lighton & Fielden 1995). Among the arachnids, ticks and scorpions appear to have very low metabolic rates compared to other arthropods (Lighton & Fielden 1995; Lighton et al. 2001). Ticks are ectoparasites that rarely encounter food and spend little time actually on their hosts. Thus a low metabolic rate is likely an adaptation to the extreme sit-and-wait strategy employed by ticks (Lighton & Fielden 1995). In scorpions, it has been suggested that their low metabolic rate is due to the cannibalistic life-style of some species (Lighton et al. 2001). In addition, variation among groups of spiders suggests a similar pattern (Anderson & Prestwich 1982; Anderson 1994, 1996).

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Therefore, it appears that life-style is in some way associated with metabolic rate.

Male and female spiders exhibit quite different behaviors that are likely the result of different selective pressures acting on each sex (e.g., Walker & Rypstra 2001, 2002). For example, there is likely strong selection on females to maximize their energy intake whereas male spiders should maximize their encounter rate with females. This results in female spiders being more aggressive towards prey and having larger chelicerae and fangs to subdue prey than males (Walker & Rypstra 2002). Numerous studies have examined metabolic rates in spiders (see references above) or sexual dimorphism (e.g., Vollrath & Parker 1992; Prenter et al. 1999; Moya-Laraño et al. 2002; Walker & Rypstra 2003), but few have examined sex differences in the metabolic rate of spiders (e.g., Kotiaho 1998). The studies that have examined sex differences in basal metabolic rate have come to different conclusions regarding which sex has a higher metabolic rate. For instance Kotiaho (1998) found that female *Hygrolycosa rubrofasciata* (Ohlert 1865) have a higher metabolic rate than males. However, in *Linyphia litigiosa* (Keyserling 1886) and in *Pardosa astrigera* (L.

Koch 1878) males have higher metabolic rates than females (Tanaka & Itô 1982; Watson & Lighton 1994). These differences may be due to differences in when the animals were tested (e.g., before or after copulation) or may reflect species-specific sex differences in the metabolic rate of males and females.

Hogna helluo (Walckenaer 1837) and *Pardosa milvina* (Hentz 1877) are two species that co-occur in many different habitats across the Eastern United States (Dondale & Redner 1990). *Hogna helluo* females construct retreats while males do not. In addition, *H. helluo* are larger and more sexually dimorphic in size and activity compared to *Pardosa milvina* (Walker et al. 1999a; Walker & Rypstra 2002, 2003). *Pardosa milvina*, on the other hand, does not exhibit as large a degree of sexual size dimorphism, males and females are similar in their activity, and females do not construct retreats. One other interesting difference between *H. helluo* and *P. milvina* is that females respond differently to food deprivation (Walker et al. 1999a, b). Activity levels in *H. helluo* increase with food deprivation and only well fed females are likely to build retreats (Walker et al. 1999a, b). However, activity levels of *P. milvina* are not influenced by feeding regime (Walker et al. 1999b). This observation led us to hypothesize that *P. milvina* will have a higher resting metabolic rate than *H. helluo*. Here we test this hypothesis and determine the degree of sexual dimorphism in resting metabolic rate for *H. helluo* and *P. milvina*. Since interspecific differences in metabolic rate correlate with life–style, we predict that male *H. helluo* will have higher rates of metabolism than female *H. helluo* and that male and female *P. milvina* will have similar metabolic rates because of their similarity in activity.

METHODS

Hogna helluo and *Pardosa milvina* were field collected as sub-adults from the Ecology Research Center (Butler County, Ohio, USA at 39.5°N and 84.7°W) in the fall of 1998. Spiders were maintained in plastic soufflé cups (100 mL for *Pardosa*, 300 mL for *Hogna*) with 1–3 cm of peat moss for substrate and were held at 25 °C, 60–70% relative humidity on a 14 Light:10 Dark light cycle until they reached sexual maturity (see Walker et al. 1999a). Spiders were generally between two and three weeks post adult molt when tested. Spiders were fed to satiation one week prior to measurement of metabolic rate and none of the spiders used in this experiment had mated. All spiders were weighed before and after respirometry. Weight loss was typically 1.8% of the initial mass. The initial weight was used in calculations of metabolic rate. Spiders were given 4 h to acclimate to 20 °C before metabolic rate was measured. We utilized 20 °C as opposed to 25 °C because of the upper limit on the water bath used to maintain a constant temperature of the air flowing through the respirometer. Voucher specimens of both species are available from the Hefner Zoology Museum at Miami University.

We measured metabolic rate using a TR-3 respirometry system (Sable Systems Inc.). This system includes both a carbon dioxide (LiCor 6252) and oxygen analyzer (FC-1B) and signal conditioners to reduce electrical noise. A multiplexor interfaced to DATACAN data acquisition/analysis software (Sable Systems Inc.) allowed switching between eight individual respirometry chambers. Metabolic rates were measured using closed-system respirometry using outdoor air. The chamber was initially purged with air free of water vapor and carbon dioxide, the chambers were left closed for a standard 30 min period, and then the air was drawn from the chambers and through the analyzers (flow rate = 50 mL·min^{-1}). Carbon dioxide production and oxygen depletion between the initial and final sampling were estimated via integration (DATACAN software) and used to calculate metabolic rates over the time interval. Spiders were observed during the period of recording and individuals that exhibited high levels of activity (e.g., if they exhibited anything other than slow walking) were not used in the analysis.

Data are presented as means ± one standard error. Ten individuals were measured of each sex from both species. Differences between the sexes in mass, carbon dioxide accumulation or oxygen consumption in μL·h^{-1}, and mass specific metabolic rates (μL·g^{-1}·h^{-1}) were examined utilizing a two-factor ANOVA with sex and species as factors. Comparisons among means were done utilizing a Tukey-Kramer procedure (Sokal & Rohlf 1995). Utilizing mass specific metabolic rates assumes

Table 1.—Mean ± S.E. for live body mass and metabolic rate measurements made on male and female *Hogna helluo* and *Pardosa milvina*. Different letters in a column indicate significant differences between sex-species combinations based on a Tukey-Kramer multiple comparison procedure.

Sex-Species Combination	Mass (mg)	$\mu LO_2 \cdot h^{-1}$	$\mu LCO_2 \cdot h^{-1}$	$\mu LO_2 \cdot g^{-1} \cdot h^{-1}$	$\mu LCO_2 \cdot g^{-1} \cdot h^{-1}$
Male *H. helluo*	198 ± 14 A	26.4 ± 1.2 A	17.3 ± 1.0 A	183 ± 19 A	138.3 ± 10 A
Female *H. helluo*	617 ± 74 B	88.8 ± 8.0 B	63.2 ± 6.8 B	206 ± 20 A	144.3 ± 12 A
Male *P. milvina*	13.3 ± 0.5 C	7.8 ± 1.2 C	4.39 ± 0.6 A	647.4 ± 75 B	572 ± 76 B
Female *P. milvina*	21.0 ± 1.2 D	6.1 ± 0.6 C	4.28 ± 0.5 A	404 ± 43 C	289 ± 23 A

isometry which may or may not be appropriate. However, these comparisons and the means of these data are presented to allow easy comparison with earlier studies of metabolic rates. To control for differences in body size without assuming an isometric relationship between body mass and metabolic rate we utilized an ANCOVA with the base-ten log

Figure 1.—Relationship between log-transformed metabolic rate (CO_2 production or O_2 Consumption $\mu L \cdot h^{-1}$) and body mass for male and female *H. helluo* (squares) and *P. milvina* (triangles). Males are shown by solid symbols and females shown by open symbols.

of body mass as the covariate, sex and species as factors and the base-ten log of carbon dioxide accumulation or oxygen consumption in $\mu L \cdot h^{-1}$ as the response variable (Packard & Boardman 1988).

RESULTS

Females were significantly heavier than males in both species but the difference between males and females was much larger for *H. helluo* compared to *P. milvina* (Table 1, Sex * Species Interaction $F_{(1,36)} = 15.14$, $P < 0.001$). There were also significant differences in metabolic rate ($\mu L \cdot h^{-1}$, Table 1, CO_2 Production, Sex * Species Interaction $F_{(1,36)} = 61.6$, $P < 0.001$; O_2 consumption, Sex * Species Interaction $F_{(1,36)} = 44.9$, $P < 0.0001$) and mass-specific metabolic rate ($\mu L \cdot g^{-1} \cdot h^{-1}$) among the sex-species combinations based on a two-way ANOVA (Table 1; CO_2 Production, Sex * Species Interaction $F_{(1,36)} = 13.15$, $P = 0.009$; O_2 consumption, Sex * Species Interaction $F_{(1,36)} = 8.64$, $P = 0.0057$).

The allometric relationship between body mass and metabolic rate differed between species for both CO_2 Production and O_2 Consumption (log(mass) * Species Interaction CO_2: $F_{(1,32)} = 7.99$, $P = 0.008$; O_2: $F_{(1,32)} = 5.23$, $P = 0.029$). In particular, metabolic rate increased with body mass in *P. milvina* but was not related to body mass in *H. helluo* (Fig. 1). Because of the species differences in the relationship between body mass and metabolic rate (i.e., the slopes are different, so comparisons of intercepts would be meaningless), we compared metabolic rates between the sexes using a separate ANCOVA for each species with log mass as the covariate and sex as a factor. There were no significant interactions between sex and log(mass) for any of the four ANCOVA's ($F_{(1,16)} < 3.07$, $P > 0.09$) indicating that the allometric coefficients re-
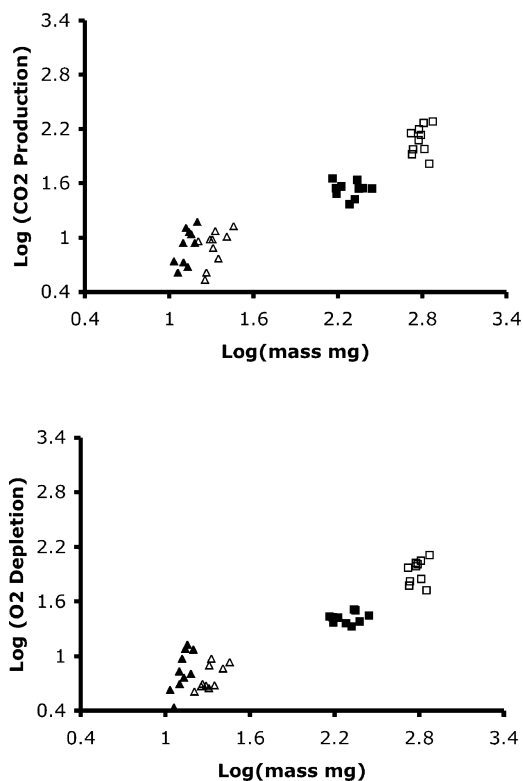
lating metabolic rate to log transformed mass were not significantly different between the sexes. In the final analyses below, the interaction terms were not included. Given that these data span a small range of adult sizes and small sample size, estimates of the allometric coefficients may not be informative. However, it is important to note that metabolic rate increased faster with body mass in *Pardosa* compared to *Hogna* (Fig. 1). In *P. milvina*, males had a higher metabolic rate than females (Fig. 1; ANCOVA CO_2 Production, $F_{(1,17)} = 12.43$, $P = 0.0026$; O_2 consumption, $F_{(1,17)} = 8.91$, $P = 0.0083$) and in *H. helluo*, females had a higher metabolic rate than males (Fig. 1; ANCOVA CO_2 Production, $F_{(1,17)} = 5.63$, $P = 0.0297$; O_2 consumption, $F_{(1,17)} = 6.51$, $P = 0.0206$).

DISCUSSION

Hogna helluo, a typical sit-and-wait predator, had a lower metabolic rate than did *P. milvina*, a much more active species. Our data also indicate significant sexual dimorphism in metabolic rate in both *H. helluo* and *P. milvina*. Male *H. helluo* had similar mass specific metabolic rates compared to female *H. helluo*, but male *P. milvina* had higher mass specific metabolic rates than did female *P. milvina*.

Many studies have suggested associations between life-style and metabolic rate (e.g., Anderson & Prestwich 1982; Lighton & Fielden 1995). However, many of these studies examine correlations between metabolic rate and whether a group (phyla class, order or family) is presumed to be active or sedentary (Greenstone & Bennett 1980; Lighton & Fielden 1995; Lighton et al. 2001). This work has suggested that, in some cases, sit-and-wait predators do have lower metabolic rates than other comparatively sized arthropods (e.g., Lighton & Fielden 1995). However, these cases appear to be the exception not the rule. This may be due to the assumption that all species within groups are either active or sedentary when in fact they may or may not be. Our data examine differences in the metabolic rates of two species for which we have a great deal of ecological and behavioral data (Walker et al. 1999a, b; Marshall et al. 2000, 2002; Balfour et al. 2003; Buddle et al. 2003; Walker & Rypstra 2003). *Pardosa milvina* is generally more active than *H. helluo* and responds differently to periods of food deprivation sug-

gesting that the metabolic rate of *H. helluo* is lower than *P. milvina*. Our data support this hypothesis and suggest that *H. helluo* is well adapted to uncertain food supplies. It should be noted that these are only two species and our data in no way account for phylogeny (see Harvey & Pagel 1991), but these and other data (Lighton & Fielden 1995; Anderson 1996) support the hypothesis that low metabolic rates are associated with a sit-and-wait lifestyle.

Sexual dimorphism in the metabolic rate of spiders has only been documented in a few species (e.g., Kotiaho 1998). Our data and other studies indicate that sex differences in metabolic rate are not consistent across taxa. That is, in some species males have a higher metabolic rate than females whereas in others, males and females have comparable metabolic rates. In fact, our data show in *Hogna*, males and females have similar metabolic rates but in *Pardosa* males have the higher metabolic rate than females. In addition, our data suggest that these differences between the sexes in metabolic rates are not related to differences between the sexes in activity as one might predict based on the results of studies which compare active and more sedentary species. Our data are similar to results from another wolf spider, *Hygrolycosa rubrofasciata* (Kotiaho 1998) but are not consistent with sex differences in the metabolic rate in *Pardosa milvina*, *P. astrigera* and *Linyphia litigiosa* (this study; Tanaka & Itô 1982; Watson & Lighton 1994). In these studies, males have higher metabolic rates than females. Why then, is there so much variation in metabolic rate differences between the sexes across different species?

Kotiaho (1998) suggests that differences between his and Watson & Lighton's (1994) study are due to the time at which metabolic rates were measured. Watson and Lighton (1994) measured the metabolic rate of males after copulation whereas Kotiaho (1998) measured metabolic rate in males that had not copulated. This is not a factor in our study since all individuals were unmated. The second reason that Kotiaho (1998) suggests is that females in the different studies may have been in different reproductive states. That is, the metabolic rate of reproductive females is likely higher than non-reproductive females and different studies may have used females

that were not all in the same reproductive state. As adults, female *P. milvina* and *H. helluo* are adults for only one season and reproduce during the summer or early fall. Our spiders matured in the lab under conditions that mimicked the light and temperature cycle of the summer months when both species are reproductively active and thus females of both species should be in a similar reproductive state. Therefore, we feel it is unlikely that species differences in sexual dimorphism for metabolic rate can be explained by differences in the reproductive state of the females.

Sex differences in metabolism likely reflect differential selective pressures acting on males and females either due to differences in their reproductive roles and/or sexual selection. This logic has been used to explain sexual dimorphism in many different morphological and behavioral characteristics (e.g., Shine 1989; Fairbairn 1997) and could likely be used to explain sex differences in metabolism. However, we do not know enough about the physiological differences between males and females, especially the relative amounts of metabolically active tissues, to accurately predict sexual dimorphism in metabolic rate or to speculate regarding the functional and/or adaptive significance of these differences. Assuming that the sexes are created equal, we hypothesized male *H. helluo* should have a higher metabolic rate than female *H. helluo*. However, by definition males and females are different. Females have ovaries, males have testis, females accumulate more lipids than males, and it is likely that the venom glands in females are larger than those of males (Foelix 1996; Walker & Rypstra 2001). Also, do we speculate that the higher metabolic rate of male *P. milvina* is due to sexual selection (e.g., Watson & Lighton 1994) or do we suggest that female mass-specific metabolic rate is lower because of a greater proportion of metabolically inactive tissues (e.g., lipids)? Hypotheses trying to explain the nature of sex differences in metabolic rate will require integrating physiological, ecological and behavioral data.

It appears that species-specific differences in metabolic rate could be related to differences in activity. However, differences between the sexes in metabolic rate are not so easily explained. Sex differences reflect the action of differential selection pressures acting on males and females and sexual dimorphism in metabolic rate likely reflects the differential effects of sexual and natural selection on males and females and may not be due to the same mechanisms that result in species specific differences. Sexual dimorphism is a complex phenomenon that is difficult to explain and this may be particularly true of complicated physiological processes such as metabolism.

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