

Energy metabolism of male and female tarantulas (*Aphonopelma anax*) during locomotion

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Summary

We examined aerobic performance traits in male and female tarantulas (*Aphonopelma anax*). Reproductive fitness in these males relies heavily on locomotory searching to locate receptive females, which are fossorial and sedentary. Because of this dimorphism in life history, we predicted that selection in males would enhance their ability to sustain high levels of aerobic metabolism (compared with females) to support increased locomotory activity during the mating season. Rates of carbon dioxide production were measured in an enclosed variable-speed treadmill. Steady-

state rates of carbon dioxide production increased linearly within the range of sustainable aerobic speeds for both males and females. Although there was substantial variation in physiological performance traits among individuals, there were no detectable intersexual differences in maximal rates of carbon dioxide production, maximal aerobic speed, minimum transport or factorial scope.

Key words: tarantula, *Aphonopelma anax*, aerobic metabolism, performance traits, sexual dimorphism.

Introduction

Although sexual dimorphism in morphology and behavior has been extensively studied, dimorphism in physiological performance (e.g. speed, endurance, aerobic capacity, cost of transport) has seldom been examined (humans, Wells and Plowman, 1983; Pate and Kriska, 1984; Sanborn and Jankowski, 1994; beetles, Rogowitz and Chappell, 2000; squamates, Snell et al., 1988; Jayne and Bennett, 1990; Cullum, 1998; birds, Brackenbury and El-Sayed, 1985; Hammond et al., 2000). Differences in physiological performance may be expected in organisms that exhibit size and life history dimorphism because these factors can, in turn, lead to differences in energetic requirements. Such is the case with most spiders. Females maintain a larger body size over a longer life span and have a higher energetic cost associated with gamete production and, in some species, parental care (Foelix, 1996). After reaching sexual maturity, male spiders change their habits and leave their retreats or webs and search actively for females. They are relatively short-lived, and the energy used in gamete production is small (although the cumulative cost of locomotion may be high). The energetic requirements associated with these different lifestyles and mating strategies may, in turn, have led to the evolution of differential metabolic rates and physiological performance capacities between males and females (Snell et al., 1988; Pough et al., 1992; Garland, 1993; Marler and Ryan, 1996; Reinhold, 1999; Rogowitz and Chappell, 2000; Gade, 2002).

The goal of this study was to compare the metabolic rates of male and female tarantulas (*Aphonopelma anax*) during

locomotion to determine whether the sexes differed in physiological performance traits such as maximum aerobic speed (MAS), maximal rate of CO₂ production ($\dot{V}_{\text{CO}_2\text{max}}$) and minimum cost of transport (C_{min}). This species displays dimorphism in life history, which is typical of most fossorial tarantulas. Females are sit-and-wait predators that usually remain within close proximity to their burrows for their entire lives, while sexually mature males abandon their burrows and search actively for well-dispersed mates (Shillington, 2002). Males are presumably under greater selective pressure for locomotor ability and efficiency because of the importance of locomotion in their mate location strategies. As a result, we predicted that males would have a higher $\dot{V}_{\text{CO}_2\text{max}}$, reflecting a greater capacity for aerobic power output, and thus higher sustainable locomotory speeds compared with females, as well as greater locomotory efficiency (i.e. lower C_{min}).

Materials and methods

Study animals

Male and female tarantulas (*Aphonopelma anax* Chamberlin) were collected from the Chaparral Wildlife Management Area (CWMA) during May–July 2000. This 6.150 ha area is managed by the Texas Parks and Wildlife Department and is approximately 13 km west of Artesia Wells, TX, USA. Animals were transported to Oklahoma State University and maintained in the laboratory in individual 3.8 l containers under a natural photoperiod (14h:10h light:dark)

and at room temperatures of 20–25°C. Water was constantly available, and food (crickets and occasionally mealworms) was available *ad libitum* except for the week prior to metabolic measurements.

Metabolic rates during locomotion

We used an open-flow respirometry system to measure rates of CO₂ production (\dot{V}_{CO_2}) of male and female tarantulas during locomotion on a variable-speed treadmill. The treadmill was housed in a clear 31.5 cm × 17 cm × 10 cm Plexiglas chamber, and outside air was pumped under positive pressure into this chamber at a flow rate greater than 100 ml min⁻¹. The air initially passed through a Drierite/Ascarite/Drierite scrubbing column to remove both CO₂ and water before passing into the treadmill chamber. A smaller 16 cm × 11.5 cm × 6 cm animal container was held firmly in place on the belt of the treadmill inside the larger chamber. The walls of this container were in constant contact with the belt of the treadmill to minimize exchange of air between the animal container and the treadmill chamber. Air was drawn by negative pressure at 100 ml min⁻¹ (Sierra mass-flow controller) from the animal container into the CO₂ analyzer (LiCor 6251), which interfaced with a computer running analog-to-digital data-acquisition software (Sable Systems).

Tarantulas were placed in the smaller chamber and left undisturbed for 30 min. Prior to exercise, we measured resting metabolic rates (RMRs). After this rest period, the treadmill was activated at a slow speed (approximately 25 m h⁻¹). When the treadmill was initially activated, many animals displayed erratic movements, but these movements usually ceased after a few minutes as they became accustomed to the movement. With animals that continued to show erratic movement patterns and bursts of speed after 5 min, we increased the treadmill speed until evenly paced movement was achieved. \dot{V}_{CO_2} measurements were recorded only at speeds sustainable for at least 20 min in an attempt to minimize anaerobic metabolism. Steady-state \dot{V}_{CO_2} for an individual was recorded during the last 5 min of continuous locomotion at each speed.

Over time, speeds were increased until speeds were reached at which the animals could not maintain evenly paced locomotion for a 20 min period. If animals stumbled at higher speeds, we reduced the speed and allowed them to regain their stride. It was then sometimes possible to increase the speed again and achieve steady-state locomotion. Speeds ranged from 25.7 to 126.3 m h⁻¹. During periods of steady-state locomotion, the treadmill was timed with a stopwatch to verify the speed. The ambient temperature during these recordings was 24–26°C.

\dot{V}_{CO_2} (ml h⁻¹) was calculated from fractional concentrations of CO₂ entering (F_I) and leaving (F_E) the respirometry chamber using the equation (from Withers, 1977):

$$\dot{V}_{\text{CO}_2} = (F_{E\text{CO}_2} - F_{I\text{CO}_2})f, \quad (1)$$

where flow rate f was in ml h⁻¹ and F_I was zero because incoming air passed through the scrubbing column. \dot{V}_{CO_2} values are presented rather than rates of O₂ consumption

because of the sensitivity of the LiCor 6251 compared with available O₂ analyzers. This is especially important when, as is the case with tarantulas, metabolic rates are low.

Maximum aerobic speed, $\dot{V}_{\text{CO}_2\text{max}}$ and minimum cost of locomotion (C_{min})

\dot{V}_{CO_2} , as with rates of oxygen consumption, typically increases with speed in a linear manner until $\dot{V}_{\text{CO}_2\text{max}}$ is reached (Bennett, 1982; Gatten et al., 1992; Full, 1997). $\dot{V}_{\text{CO}_2\text{max}}$ occurs at MAS, which is the maximal speed that can be sustained aerobically, and C_{min} is the slope of the line determined from the regression equation relating \dot{V}_{CO_2} to speed (Taylor et al., 1970; Bennett, 1982). We defined $\dot{V}_{\text{CO}_2\text{max}}$ for each individual as the \dot{V}_{CO_2} at which an increase in speed resulted in no significant increase in \dot{V}_{CO_2} . This was determined from examination of plots of \dot{V}_{CO_2} versus speed for each individual. Metabolic rates in the anaerobic range were not related to speed ($r=0.45$, $P=0.19$) and were excluded from analyses.

For comparison of our results with previous studies in which metabolic rates were reported as mass-specific rates of oxygen consumption (mass-specific \dot{V}_{O_2}), we converted the raw data from \dot{V}_{CO_2} to \dot{V}_{O_2} using a respiratory quotient (RQ) of 0.92 (C. Shillington, unpublished data). For each individual, we replotted the relationship between metabolic rate and speed (km h⁻¹), this time using mass-specific \dot{V}_{O_2} (ml g⁻¹ h⁻¹), and determined C_{min} (ml O₂ g⁻¹ km⁻¹) from the regression analyses.

Results

Comparison among individuals

Prior to activating the treadmill, we attempted to measure RMRs. However, several animals continuously explored the chamber during this time so, for these individuals, we used RMRs determined previously (Shillington, 2001). Previously measured RMRs were similar to RMRs measured on the treadmill for the animals that remained quiescent ($N=5$, paired $t=-0.78$, $P=0.50$).

The behavior of tarantulas on the treadmill closely resembled natural locomotion (C. Shillington, personal observation). Typically, movement was initiated when the trailing legs made contact with the back of the treadmill chamber. Sometimes this contact resulted in quick bursts of locomotion; however, most animals soon adjusted to the movement of the treadmill. Steady-state \dot{V}_{CO_2} (ml CO₂ h⁻¹) increased with increasing speed for both males and females (repeated-measures analysis of covariance, ANCOVA, with body mass as covariate: $F_{4,21}=19.07$, $P<0.01$).

From regression analyses of the relationship between \dot{V}_{CO_2} (ml h⁻¹) and treadmill speed (m h⁻¹) (Fig. 1), we obtained a y-intercept and slope (C_{min}) (Table 1). One male and three females achieved anaerobic speeds (indicated in Table 1 and Fig. 1). For the remaining animals, \dot{V}_{CO_2} increased linearly to the fastest speed achieved, so $\dot{V}_{\text{CO}_2\text{max}}$ and MAS are probably underestimated. The maximum speed reached by any individual on the treadmill was 126.3 m h⁻¹, and this was achieved by a 14 g female. Although this speed appeared to be

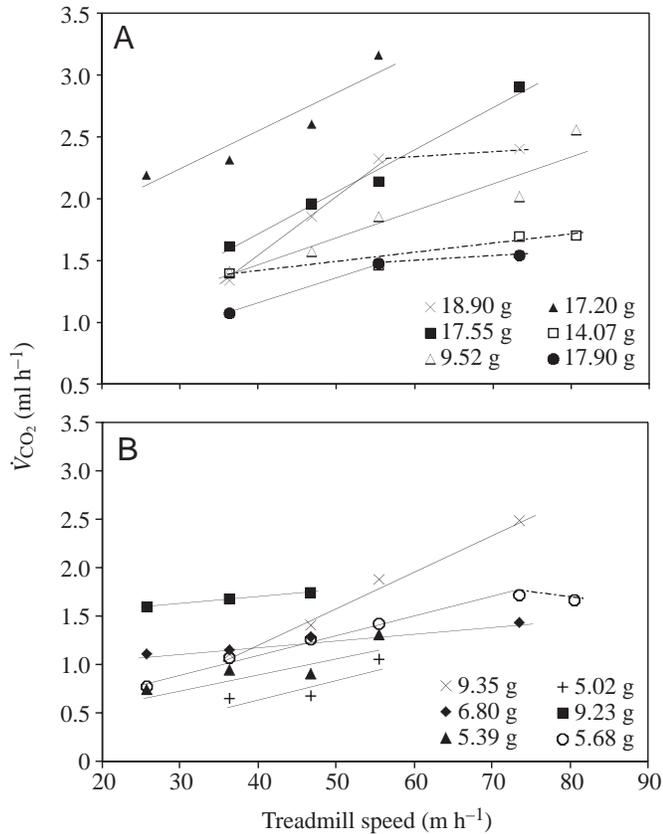


Fig. 1. \dot{V}_{CO_2} (ml h^{-1}) for female (A) and male (B) tarantulas as a function of treadmill speed. Individual data points are shown for each animal, and the corresponding body mass is indicated. Least-squares linear regression lines are shown for aerobic (solid lines) and anaerobic (broken lines) speeds. The highest anaerobic speed of 126.3 m h^{-1} achieved by the 14 g female is not shown (see Table 1). Individual results are based on single measurements at each speed.

well within her anaerobic range ($\text{MAS}=36.4 \text{ m h}^{-1}$), she sustained this level of activity for approximately 20 min. More typically, animals were not able to maintain even-paced locomotion on the treadmill above MAS, and they either stumbled continuously or climbed partially onto the walls of the animal container to escape the moving treadmill.

C_{min} differed among individuals for both sexes (test for homogeneity of slopes: females, $F_{5,12}=22.04$, $P<0.01$; males, $F_{5,12}=13.48$, $P<0.01$), and the y-intercepts were, on average, approximately twice the RMRs (Table 1). For one female (14.07 g), it was not possible to determine a slope because she appeared to be using anaerobic metabolism at all but the lowest speed. For both males and females, log-transformed C_{min} showed a weak tendency to increase with increasing log-transformed body mass ($r=0.56$, $P=0.08$).

Intersexual comparisons

We compared $\dot{V}_{\text{CO}_2\text{max}}$ (ml h^{-1}), factorial scope (maximal rate of CO_2 consumption/RMR), C_{min} ($\text{ml CO}_2 \text{ m}^{-1}$) and MAS (m h^{-1}) between males and females. Prior to analyses, we log-

transformed these variables and tested for the effect of body mass (also log-transformed), but body mass was not a covariate of any variable. Analysis of variance (ANOVA) detected no sexual dimorphism in $\dot{V}_{\text{CO}_2\text{max}}$ ($F_{1,10}=3.22$, $P=0.10$), factorial scope ($F_{1,10}=0.36$, $P=0.56$), MAS ($F_{1,10}=0.19$, $P=0.16$) or C_{min} ($F_{1,9}=3.88$, $P=0.08$).

Submaximal \dot{V}_{CO_2} values (ml h^{-1}) were compared between males and females at three speeds for which there was a minimum of three individuals from each group. Because body mass was a covariate of \dot{V}_{CO_2} within speeds, and mass-scaling slopes [$\log_{10}\dot{V}_{\text{CO}_2}$ versus $\log_{10}(\text{body mass})$] were homogeneous for males and females at each of the three speeds, we used an ANCOVA; \dot{V}_{CO_2} was similar between males and females at each speed (Table 2).

Discussion

The main purpose of this study was to determine whether differences in life history between the sexes in tarantulas (specifically increased locomotory activity in males) would correspond with sexual dimorphism in performance and exercise capacity.

Metabolic rates during locomotion

Within the range of sustainable speeds, \dot{V}_{CO_2} increased with increasing speed in both male and female *A. anax* (Fig. 1). A similar linear increase in \dot{V}_{O_2} and \dot{V}_{CO_2} is typical of other invertebrates (Full, 1997; cockroaches, Herreid, 1981; Herreid and Full, 1984; crabs, Full, 1987; beetles, Lighton, 1985; Rogowitz and Chappell, 2000) and vertebrates (Taylor et al., 1970, 1982; Bennett, 1982; Taylor and Heglund, 1982; Gatten et al., 1992).

There were some behavioral differences between the sexes in relation to locomotion on the treadmill. Females were typically more resistant to running at higher speeds and usually wedged themselves against the side walls of the animal container as speeds increased above a slow walk. However, this does not necessarily indicate an inability to move at higher speeds; one 14 g female attained a speed of 126.3 m h^{-1} . In addition, large females with a big abdomen tended to hold their body closer to the ground, whereas smaller, lighter females and males had a more elevated posture during locomotion. Only three of the six females reached speeds at which they became anaerobic; thus, empirical $\dot{V}_{\text{CO}_2\text{max}}$ may underestimate the performance ability of these animals if they stopped their locomotory activity behaviorally before reaching physiological MAS.

Males moved more readily on the treadmill and were typically active within the animal chamber during the 30 min rest period prior to exercise. These differences are consistent with observations of males and females maintained in the laboratory (C. Shillington, personal observation). Although males had a smaller abdomen and longer legs compared with females (C. Shillington, unpublished data), MAS of males was very similar to that of females. Only one of six males reached an anaerobic speed (Fig. 1), suggesting that empirical MAS

Table 1. Resting metabolic rate, \dot{V}_{CO_2} and linear regression statistics for the relationship between treadmill speed and \dot{V}_{CO_2} in individual tarantulas

Mass (g)	RMR ($\mu\text{l CO}_2 \text{ h}^{-1}$)	$\dot{V}_{CO_2\text{max}}$ ($\mu\text{l CO}_2 \text{ h}^{-1}$)	Factorial scope	MAS (m h^{-1})	y-intercept [†] ($\mu\text{l CO}_2 \text{ h}^{-1}$)	Slope, C_{min} [†] ($\mu\text{l CO}_2 \text{ m}^{-1}$)	C_{min} ($\text{ml O}_2 \text{ g}^{-1} \text{ km}^{-1}$) [‡]
Males							
9.35	156.1	2486.85	15.93	73.44	-308.83±154.27	38.25±2.82	4.45
6.80	195.5	1432.66	7.33	73.44	925.36±43.12	7.02±0.88	1.15
5.39	139.2	1312.95	9.43	55.44	300±267.59	16.48±6.29	3.32
5.02	131.2	1060.42	8.08	55.44	-165.68±555.53	20.83±11.86	4.59
9.23	204.2	1882.95	9.22	46.80	1356.19±64.33	9.01±1.51	1.06
5.68	116.2	1722.62	14.82	73.44*	319.97±59.00	19.51±1.17	3.65
Mean	6.91	157.07	10.80	63.00	404.50	18.52	3.04
Females							
18.90	183.5	2323.17	12.54	55.44*	-539.06±61.78	51.48±1.32	2.96
17.55	296.1	2899.30	9.79	73.44	324.81±160.47	34.45±2.93	2.13
9.52	100.1	2556.22	25.53	80.64	530.36±262.78	23.09±4.32	2.64
17.20	207.6	3162.01	15.23	55.44	1275.27±343.66	31.48±8.08	1.99
14.07	192.0	1392.64	7.25	36.36*	-	-	-
17.90	237.4	1472.28	6.20	55.44*	301.32	21.12	1.28
Mean	15.72	208.78	12.75	59.46	378.54	32.32	2.20

RMR, resting metabolic rate; MAS, maximum aerobic speed; C_{min} , minimum cost of transport; RQ, respiratory quotient.

*Individuals that reached anaerobic speeds.

[†]Values include the standard error of the slope and intercept.

[‡]Assumes that RQ=0.92 (see text).

and $\dot{V}_{CO_2\text{max}}$ underestimated performance ability. Conversely, males were more likely to stumble and lose balance at higher speeds compared with females, which simply refused to move. One possible explanation is the age and physical condition of the males. All males used in this study died within 6–8 weeks of the treadmill trials, suggesting that they may have been past their prime at the time of the study. Two to three weeks prior to death, males became noticeably uncoordinated to the point where they could not capture crickets easily for feeding. Although there was little or no stumbling by males at lower speeds on the treadmill during the trials, the uncoordinated movements and stumbling observed at high speeds may have been related to their age and physical condition. This idea is further supported by the observation that one male tarantula freshly collected in Oklahoma (unidentified species but

approximately the same size as *A. anax*) was able to sustain a speed of 150.5 m h^{-1} (\dot{V}_{CO_2} =0.35 ml h^{-1}) for more than 20 min without stumbling, which is 2–3 times the speeds achieved by any of the males in the present study. However, these high speeds were anaerobic; MAS and $\dot{V}_{CO_2\text{max}}$ for the Oklahoma male were similar to those of *A. anax* males. In addition, the Oklahoma male survived more than 6 months beyond the completion of this study.

Maximum rates of aerobic respiration

Maximum rates of aerobic respiration have been reported for females of two other tarantula species (Theraphosinae, species unknown; Herreid, 1981; *Brachypelma smithi*, Anderson and Prestwich, 1985). $\dot{V}_{O_2\text{max}}$ is similar between *A. anax* and the

Table 2. Comparisons of \dot{V}_{CO_2} of male and female tarantulas (*Aphonopelma anax*) walking at three submaximal speeds

Treadmill speed (m h^{-1})	\dot{V}_{CO_2} (ml l^{-1})		F	P
	Females (N)	Males (N)		
36.36	1.52±0.17 (6)	1.10±0.14 (6)	0.06	0.81
46.80	2.00±0.22 (4)	1.21±0.15 (5)	0.19	0.68
55.44	2.19±0.28 (5)	1.51±0.16 (5)	0.08	0.78

Values are means ± S.E.M.

F values are from an analysis of covariance with the body mass as covariate.

Table 3. Locomotor energetics reported for females of three species of tarantula at similar temperatures (23–25°C)

Species	Mean mass (g)	$\dot{V}_{CO_2\text{max}}$ ($\mu\text{l CO}_2 \text{ h}^{-1}$)	C_{min} ($\mu\text{l CO}_2 \text{ m}^{-1}$)
<i>Aphonopelma anax</i> (present study)	15.72	2301	32.32
Unknown (Herreid, 1981)	12.7	2220	5.02
<i>Brachypelma smithi</i> (Anderson and Prestwich, 1985)	26.92	4210	-

C_{min} , minimum cost of transport.

For comparison, data were converted to units of whole-animal \dot{V}_{CO_2} using a respiratory quotient of 0.92.

unknown tarantula species studied by Herreid (1981) (Table 3). Although there has been one study of metabolic rates during activity in male tarantulas (Seymour and Vinegar, 1973), few raw data were reported. Tarantulas fatigued within 2–7 min (depending on temperature) in that study, suggesting that they were beyond maximal aerobic activity.

Minimum cost of transport (C_{\min})

C_{\min} is widely used in interspecific comparisons but is conventionally reported in mass-specific units of oxygen consumption ($\text{ml O}_2 \text{g}^{-1} \text{km}^{-1}$; Table 1). Interspecific comparisons among diverse taxa show that mass-specific C_{\min} decreases with increasing body mass (mammals and birds, Taylor et al., 1982; reptiles, Bennett, 1982; insects, Herreid, 1981; Lighton, 1985; crustaceans, Full, 1987). However, expression of C_{\min} in mass-specific units is a longstanding convention for which we can think of no good justification (see Altmann, 1987); therefore, we base our comparisons on the whole-animal units we actually measured.

Mean C_{\min} for both male and female tarantulas was very similar to predicted values calculated using the C_{\min} /mass scaling equation determined for several insect taxa (Lighton 1985) (Table 4). The C_{\min} /mass scaling equation provided by Gatten et al. (1992) includes data from more diverse taxa (e.g. birds, mammals, reptiles, crustaceans and insects); the predicted C_{\min} is again similar to our values (Table 4). However, a previous study reported a C_{\min} for tarantulas that was approximately a factor of 10 lower than C_{\min} measured for *A. anax* (Herreid, 1981) (Table 3). Tarantulas in this previous study ran at substantially higher velocities (100–250 m h^{-1}) than in our study, and Herreid (1981) suggests that there may have been a large anaerobic contribution, leading to the exceptionally low estimate of C_{\min} . Similarly, Anderson and Prestwich (1985) ran tarantulas at higher speeds, which they acknowledged as supermaximal. We therefore suggest that our values are the first reliable measurements of submaximal C_{\min} in a large spider.

Table 4. Comparison of C_{\min} for male and female *Aphonopelma anax* measured in this study with values determined from interspecific arthropod data (Lighton, 1985) and interspecific vertebrate and invertebrate data (Gatten et al., 1992)

	C_{\min} ($\mu\text{l CO}_2 \text{m}^{-1}$)	
	Females (mass 15.72 g)	Males (mass 6.91 g)
Empirical C_{\min} (this study)	32.32	18.52
Predicted C_{\min} (Lighton, 1985)	30.08	16.97
Predicted C_{\min} (Gatten et al., 1992)	27.19	15.96

C_{\min} predicted for a 6.91 g male and a 15.72 g female tarantula were converted from their original units to $\mu\text{l CO}_2 \text{m}^{-1}$ using a respiratory quotient of 0.92 and joule/ CO_2 coefficients from Gessman and Nagy (1988).

C_{\min} , minimum cost of transport.

We noted substantial variation in estimated C_{\min} among individuals (Table 1). Intraspecific variation in C_{\min} has seldom been analyzed, although such variation is typical of studies that report data for individuals (e.g. Secor et al., 1992; Walton et al., 1994; Autumn et al., 1999). Walton et al. (1994) found that C_{\min} was independent of body mass for northern toads (*Bufo boreaus halophilus*). Similarly, there was only a weak relationship between mass and C_{\min} in *A. anax*. Neither the mechanistic explanation nor the behavioral consequences of such individual variation in apparent locomotor economy are known.

Sexual dimorphism in metabolic rates and performance traits

In eucalyptus-boring beetles, Rogowitz and Chappell (2000) reported substantially higher active metabolic rates and factorial scope in male beetles compared with females of the same species. These differences are consistent with the higher-energy lifestyle of adult males involving very active mate-seeking behavior, in which high running speeds play an important role in mating success (Rogowitz and Chappell, 2000). We predicted similar results for tarantulas because of the higher-energy lifestyle of adult males compared with females.

Analyses of submaximal \dot{V}_{CO_2} during activity, $\dot{V}_{\text{CO}_2\text{max}}$, C_{\min} and MAS indicated no sexual dimorphism in these traits. Any differences in the means of these values (Table 1) are due to differences in the mass of males and females. The capacity for high rates of energy expenditure requires a high rate of oxygen consumption (and CO_2 production) as well as a high capacity to deliver oxygen from the lungs (i.e. well-developed lungs, a good circulatory system and a high maximal heart rate) (Garland, 1993). Anderson and Prestwich (1982) suggest that tarantulas have a limited activity capacity because of their relatively inefficient book lungs and open circulatory system. In addition, hemocyanin in tarantula blood binds less oxygen than does hemoglobin (Paul, 1992). Thus, males may be physiologically incapable of a higher $\dot{V}_{\text{CO}_2\text{max}}$ despite having a higher RMR compared with females (Shillington, 2001). Additional research is needed to address questions related to physiological limitations and also to examine the potential influence of age and physical condition on the performance of male and female tarantulas.

Endurance capacity was not measured during these trials and this would be an interesting comparison between males and females. Observations of males in the field indicated that they maintained relatively low locomotory speeds (approximately 40–70 m h^{-1}) for many hours at a time (C. Shillington, unpublished data), interrupted intermittently by relatively brief pauses. Although increased endurance capacity is typically correlated with increased \dot{V}_{CO_2} , locomotor behavior patterns are also important for defining performance limits. Intermittent movement patterns (i.e. frequent transitions from rest to exercise and *vice versa*) can increase the total distance traveled before fatigue (Full and Weinstein, 1992; Weinstein and Full, 1998, 1999; Kramer and McLaughlin, 2001). Because maximum speed may not be as important as endurance for

male tarantulas, this is one possible mechanism that may allow them to maintain prolonged searching activity despite their physiological constraints.

Further studies are needed to determine the effects of age on physiological performance and to examine the role of anaerobic metabolism in active male and female tarantulas. Data from one male (freshly collected Oklahoma species) and one female suggest that these animals may be capable of sustaining anaerobic speeds for long periods. Many invertebrates use a mixture of aerobic and anaerobic energy sources even at submaximal speeds (Full, 1997), and individual differences in recruitment of anaerobic pathways may contribute to empirical variation in apparent C_{min} .

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