THERMAL ECOLOGY AND ENERGETICS

OF A TEXAS TARANTULA

(APHONOPELMA ANAX)

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PREFACE

All three chapters in this dissertation are written for submission for publication in the journals, Canadian Journal of Zoology, Physiological and Biochemical Zoology, and Journal of Experimental Biology respectively. Formatting conventions for headings, references, tables and figures follow "Instructions for Contributors" from each journal.

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TABLE OF CONTENTS

Chapter Page

LIST OF TABLES

Table Page

LIST OF FIGURES

Figure Page

CHAPTER 1

THERMAL ECOLOGY OF MALE TARANTULAS (*APHONOPELMA ANAX*) DURING THE MATING SEASON

Abstract – During the mating season, male tarantulas completely abandon their burrows and actively search for widely distributed females, which remain fossorial. As a result, males are exposed to larger fluctuations in environmental conditions without the protection of a permanent retreat. Body temperatures (T_bs) of active male tarantulas encountered fortuitously in the field ranged from 24.7 – 35.1 °C and preferred T_bs measured in a laboratory thermal gradient ranged from 22.1 – 31.3°C. The thermal options available to males at random points within their environment varied substantially throughout the day but typically reached temperatures greater than 40 °C. In comparison, temperatures within burrows remained below 40 °C. Indices calculated from these temperature data suggested that males thermoregulated effectively during the day, while at night environmental temperatures were within their preferred T_b range and so there was no need to actively regulate their T_bs.

In addition, I determined the exact times that males ceased locomotor activity in the morning (retreat) and when they started activity in the evening (emergence). Data from 29 radiotagged males indicated that they retreated into temporary burrows between 06:47 and 10:53 CST. Activity commenced again between 16:36 and 20:53 CDT once temperatures reached 29.1 to 38.8 °C, which is close to their preferred or selected T_b range.

Introduction

For ectothermic animals, biological processes are dependent either directly (by changing rates of biological reactions) or indirectly (e.g., costs of thermoregulation) on body temperatures (T_b), which in turn depend on environmental temperatures. Many ectotherms live in thermally variable environments, so their T_bs are also subject to variation and this resulting variation in T_b affects most physiological and developmental processes such as feeding, digestion, growth, locomotion, mating and reproduction (Kingsolver 1989; Huey 1991; Casey 1992; Peterson et al. 1993). Thermoregulation implies an active regulatory process in which animals attempt to maintain their T_bs as close as possible to some preferred T_b range. Thus, the extent to which ectotherms thermoregulate reflects a combination of relative costs and benefits associated with such behaviors (Huey and Slatkin 1976, Shine et al. 2000).

Although the ability to regulate body temperature (thermoregulation) is well documented in a variety of vertebrate and invertebrate ectotherms (reviewed in Avery 1982; Heinrich 1981; Peterson 1987; Peterson et al.1993), spiders as a group have received comparatively little attention in this area. Spiders have been shown to regulate T_b via behavioral mechanisms. These mechanisms include orientation (mostly orb weavers) (Carrel 1978; Casey 1981; Cloudsley-Thompson 1991, 1993), changing their position within a burrow (fossorial spiders) (Baerg 1958; Humphreys 1974, 1978; Minch 1978; Seymour and Vinegar 1973; Lubin and Henschel 1990), restricting activity to cooler parts of the day (Minch 1978; Punzo and Henderson 1999) and evaporative cooling (Davies and Edney 1952; Chew 1961; Pulz 1987; Punzo and Jellies 1983). In addition, spiders have been shown to select retreat sites based on the thermal properties

of the environment (Riechert and Tracy 1975; Riechert 1981, 1985; Hammerstein and Riechert 1988) because thermal factors influence activity times and this can have major impacts on behavior and ecology.

Male tarantulas of North America represent an interesting case for studying thermoregulation because of their change in life history once they reach sexual maturity. As juveniles and sub-adults, both males and females are fossorial, sit-and-wait predators. Females remain fossorial throughout their entire life cycle and may inhabit the same burrow for many years, maybe even their entire life (approximately 20 years) (Baerg 1958). However, once males reach sexual maturity, they abandon their burrows and search actively for widely dispersed females (Thornhill and Alcock 1983; Shillington and Verrell 1997). Movement during this time appears to be relatively random (Janowski-Bell and Horner 1999), and males compete via scramble competition for access to receptive females (Shillington and Verrell 1997).

Although females live and continue to mate for many years after reaching sexual maturity, males live for approximately 9 months (in the laboratory) after their maturing molt. However, in the wild, this period for males is probably much shorter on average because of exposure to predators. Additionally, although males restrict their searching activity to the cooler parts of the day (Minch 1978; Punzo and Henderson 1999), they are likely exposed to larger fluctuations in environmental conditions than females and, without the protection of a permanent burrow, are more vulnerable to heat stress and desiccation (Seymour and Vinegar 1973; Punzo 1991).

Constraints on activity times have been investigated in many ectothermic animals (Huey 1982; Peterson 1987; Grant and Dunham 1988; Warburg and Polis 1990;

Cloudsley-Thompson 1991). In arid regions, rhythmic locomotory activity is well studied and emergence from and retreat into burrows is influenced by environmental factors and biological clocks (reviewed in Cloudsley-Thompson 1991). Variation in patterns of temporal activity are usually a response to specific environmental conditions and may be related to the organism's physiological adaptations.

I worked with a species of tarantula from southern Texas (*Aphonopelma anax*) and used the conceptual framework suggested by Hertz et al. (1993) to describe thermoregulation by males during the mating season and also to examine temporal patterns of emergence and retreat. To do this, I measured (1) body temperatures (T_bs) of active males, (2) available thermal options (i.e., operative temperatures, see Porter and Gates 1969; Bakken 1981, 1992) and, (3) preferred T_b range selected by males in a laboratory thermal gradient. I then calculated indices from these data to determine the extent of active thermoregulation by male tarantulas (Hertz et al. 1993). In addition, I measured light intensity and relative humidity along with air and substrate temperatures at the exact times of emergence and retreat to determine if these environmental factors influenced the timing and duration of male tarantula activity.

Although they are ideal subjects for ecological and behavioral studies because of their large size and seasonal activity, tarantulas remain a poorly studied group of animals. In this study, I attempt to quantify some of the ecophysiological aspects that relate directly to male fitness, which are not only critical to understanding tarantula ecology, but also provide an excellent opportunity for studying general questions of sexual selection and thermal biology.

Methods and materials

Study Area

During May-July 1998-2000, fieldwork was conducted at the Chaparral Wildlife Management Area (CWMA), which is located approximately 13 km west of Artesia Wells, Texas. This 6,150-ha area is contiguous across parts of Dimmit and LaSalle counties and the vegetation is a mixed-brush community dominated by mesquite *(Prosopis glandulosa)* and Acacia (*Acacia* spp.) (see Hellgren et al. 2000, for additional details). Male tarantulas *(Aphonopelma anax)* are active at this site during late May and throughout June, a period that typically coincides with peak rainfall events. Male activity decreases toward the end of June and in July and August when temperatures reach their maxima and rainfall decreases.

Body Temperature

For this study, I collected male tarantulas from established drift fences at the CWMA and I also captured animals by road cruising and fortuitous encounters. At each encounter with free-ranging males, (i.e., not animals captured in drift fence buckets), I measured three different temperatures with a 30-gauge copper-constantan thermocouple connected to a digital thermometer: (1) body temperature (T_b) (measured on the pedicle between cephalothorax and abdomen), (2) shaded air temperature (T_a) at tarantula height (approximately 2 cm above the ground) where the tarantula was first sighted and, (3) shaded substrate temperature (T_s).

For insects and arachnids, the temperature in the thorax is usually taken as a measure of T_b. However, measurement of thorax temperature requires puncturing the

exoskeleton. I wanted to reduce trauma to the animals (especially those that were radio-tagged and underwent several T_b measurements) and therefore I hypothesized that an external measurement directly on the thin pedicle between cephalothorax and abdomen would be a good indicator of internal cephalothorax T_b. Initial comparisons of internal and external T_bs indicated no difference between the two types of measurements (range of $T_{b\text{ - internal}}$: 25.5 – 31.6 °C; range of $T_{b\text{ - external}}$: 25.4 – 31.8; mean difference = 0.1°C; n = 28, paired-t = -0.91, p = 0.37). Consequently, all further T_bs were measured externally.

Selected Range of T_bs

I measured the selected range of T_bs (T_{sel}) in the laboratory in a 1.5-m linear thermal gradient using six randomly selected males. The gradient was kept in a room with a constant temperature of 15 °C and temperatures along the gradient were maintained by an electrical heating element controlled by a rheostat at one end, and a cold water bath at the opposite end. Temperatures along the gradient ranged from approximately 12 – 46 °C and fluorescent ceiling lights provided a 14:10 light:dark photoperiod. I implanted a lightweight (30-gauge) copper-constantan thermocouple in each male's cephalothorax and recorded T_bs on a datalogger (HOBO Type T Thermocouple H12-003). Males had a 1-hour acclimation period and then I started recording body temperature every 10 minutes for a 24-hour period.

Operative Temperatures

I characterized the thermal options available to male tarantulas during the day by

using exoskeletons (from captive *A. anax* maintained in the laboratory) as physical models (Chappell 1983). A thermocouple was glued into position with its sensory tip in the middle of the hollow cephalothorax region. I measured temperatures using a digital thermometer and/or dataloggers (Hobo H12-003, Onset Computer Corporation). I moved one model randomly through the environment (random relocation distances and times were generated using a stopwatch and the direction of each move was randomly determined on a compass). T_es were generated in such a manner throughout the entire field season and covering all hours from sunrise to sunset during June 2000. In addition, I obtained T_e values at half-hour intervals for the two most extreme microhabitats above ground, i.e., full sun and full shade, and I assumed that tarantulas active on the surface could achieve T_bs anywhere between these two extremes. These models were left in the same location for 24-hour periods to determine temperatures available during a typical day and night. Full-sun and full-shade measurements were obtained once a week during June 1999 and 2000, the month when males appeared to be most active. Finally, because male tarantulas usually retreated into underground refuges during the hottest part of the day, I measured temperatures of four burrows/refuges previously occupied by radio-tagged males over a 24-hour period during both years.

To test the exoskeleton model, I placed an exoskeleton with an attached thermocouple on sandy soil and allowed it to heat in moderate (early morning and evening) natural sun. A live tarantula with an implanted thermocouple was free to move in the same area. Temperatures were recorded at 10-minute intervals. Comparisons of model and tarantula during these times showed a mean difference of 0.16 °C, indicating the temperature measurements were not significantly different from each other ($n = 34$;

paired-t = -1.81, $p > 0.08$). In the morning, T_bs of the live animal tended to be lower than the exoskeleton model but in the evening, model temperatures were lower. These differences indicated that rates of heat loss and heat gain were slightly faster in the model due to lower thermal inertia of the hollow exoskeleton compared to the live animal. Overall differences between the model and live animal were slightly higher in the evening compared to the morning. The correlation between the two measurements was $r = 0.994$ ($p < 0.001$), suggesting that the model was a good indicator of tarantula T_b.

Thermoregulation Indices

I evaluated thermoregulation using the original indices suggested by Hertz et. al. (1993). Because I did not have continuous T_b readings from any of the animals, I calculated indices using the combined data set with T_bs from all the animals. The index d_b indicates the extent to which tarantulas experience T_b outside of T_{sel} and is calculated as the mean absolute deviation between T_b and the extremes of the T_{sel} range. The index d_e is an indication of the thermal quality of the habitat and is calculated as the mean absolute deviation between T_e and T_{sel}. When T_b or T_e was within T_{sel}, a deviation of zero was assigned. Finally, to address the question of how carefully tarantulas thermoregulate, I calculated the "index of effectiveness (E)": $E = 1 - (d_b/d_e)$. If the result from this equation is close to zero, this indicates no thermoregulation, while values closer to one suggest precise thermoregulation (Hertz et al., 1993).

Emergence and Retreat Measurements

I weighed and measured (carapace length and width, abdomen length, and length of all four left legs) all captured individuals. During 1999 and 2000, 23 random males

weighing more than 8.5 g were fitted with radio-transmitters (~ 0.8 g, L.L. Electronics (1998-99); ~ 0.65 g Holohil (2000)). I glued radio-transmitters to the posterior portion of the carapace after removing some of the hairs and dirt with rubbing alcohol. I released these animals close to the site of capture at approximately 04:00 (CST) and relocated them using a yagi antenna and TR-4 receiver (Telonics). The early morning release allowed plenty of time for animals to find daytime refuges before the heat of the day. During 1998 and 1999, I relocated males twice a day and measured T_b during activity on alternate days to minimize disturbance to the animal. During 1999 and 2000, I followed males closely for two consecutive days and recorded air and substrate temperature, relative humidity and light intensity (HOBO-H8 temperature/relative humidity/light intensity data logger) as soon as males left their temporary daytime refuges. Activity was often preceded by a period of alertness or movement within the burrow which was ignored. While males were active, I relocated them approximately every two hours. In the morning, I monitored these animals more closely and again recorded air and substrate temperature, relative humidity and light intensity at the exact time when males ceased activity and retreated into a new daytime refuge. I examined the data for correlations between time and the corresponding environmental variables to determine if choice of retreat and emergence times were related to changes in temperature, light levels, or humidity.

Results

Body Temperature

I encountered a total of 96 active adult tarantulas over the three summers (not including females found in burrows). Of these, 86 were males (89.6%) and 10 were females (10.4%). In general, females had larger bodies than males, but males had longer legs (Table 1.1). There was no difference between T_bs measured for males and females (Kruskal-Wallis $\chi^2 = 0.912$; $p = 0.76$); however, because of the small sample size for females, all subsequent analyses incorporate data from males only. From 58 of these males, I obtained a total of 128 T_b measurements from free-ranging males that varied from 24.7 – 35.1 °C with a mean of 29.4 °C (Fig. 1a).

The majority of T_b measurements (including both fortuitous encounters and radio-tagged individuals) were taken between sunset and sunrise (approximately 20:30 to 06:45 CST) because this is when most males were active and so they were more likely to be encountered. I found no difference between air temperatures (T_a) (at tarantula level), substrate temperatures (T_s) and T_bs that were recorded sequentially within a two-minute period of encountering or recapturing males (ANOVA: $F_{2,332} = 2.01$, $p = 0.14$). Serial measurements on individual males were assumed to be independent of one another. Typically, T_b measurements fell in between T_a and T_s (mean: $T_a = 28.6$, $T_b = 29.1$, $T_s = 29.3$).

Selected Range of T_bs

T_bs of six male tarantulas were measured over a 24-hour period in the thermal gradient. The voluntary thermal maximum (VT_{max}) was 35.1 °C and across all tarantulas

T_bs ranged from 18 – 35.1 °C (Fig. 1.1b). I discarded the data from one animal because he remained at the cold end of the gradient for the entire experimental period. Males appeared to move randomly within the gradient for the entire 24-hour period with no evidence of a nocturnal/diurnal pattern. There is currently no standardization of methods for calculating preferred or selected body temperature ranges (T_{sel}) from laboratory thermal gradients and investigators have used the central 50% (Hertz et al. 1993; Kearney and Predavec 2000), 80% (Diaz 1994; Bauwens et al. 1996) or the entire range of T_bs (Punzo 1991; Rummery et al. 1994). I estimated T_{sel} as the central 80% of all T_bs selected because this range included most major peaks in the frequency distribution of T_bs (Fig. 1.1b). So defined, T_{sel} ranged from 22.1 – 31.3 °C.

Operative Temperatures

Operative temperatures available during the day showed a daily cycle (Fig. 1.2). The temperatures of hypothetical male tarantulas moving randomly throughout the environment are shown (T_e-random) along with possible high and low extremes (full sun (T_e-sun) and full shade (T_e-shade)). In addition, temperatures available to inactive males remaining in burrows during this same period are shown (T_{burrow}). The values for T_e-sun, T_e-shade, and T_{burrow} are means for each time period based on eight total measurements (four from each year). The mean, standard error and range for each variable (data from each year were pooled) are shown in Figure 1.2. The highest temperature (73.1 °C) was recorded using the random model placed on a dark substrate in full sun, whereas the exoskeleton model exposed continuously to full sun (T_e-sun) reached a maximum temperature of only 63.2 °C. Most of the variation in T_e-sun during daytime hours (Fig.

1.2) can be attributed to intermittent cloud cover. However, even with cloud cover, temperatures of the model remained above 40 °C. T_e-random deviated widely from T_{sel} and only 16.5% of all T_e-random measurements were within T_{sel} (Fig. 1.1c).

Temperatures in the shade (T_e-shade) and in burrows (T_{burrow}) stayed relatively stable throughout the day. T_{burrow} remained below 40 °C; however, even in the shade temperatures occasionally reached above 45 °C. The range of temperatures in burrows was less than 10 °C, compared to ranges of more than 20 °C in the other microhabitats (Table 1.2).

Temperatures measured in burrows throughout the day were similar to T_{sel} determined in the laboratory thermal gradient and were seldom above VT_{max}. All operative temperatures measured at night were within T_{sel}, while T_es measured in the two extreme environments indicated that a completely sunny thermal environment deviated on average 16.91 °C above VT_{max}. During daylight hours (approximately 10:30 and 19:30 CST), T_e-sun was above VT_{max} 68% of the time. T_e-shade values were above VT_{max} between 11:30 and 14:00 CST by an average of 3.87 °C. Because shaded habitat at the field site occurred in clumps, a male tarantula moving actively through the environment during the day would experience T_bs well above VT_{max} and would risk overheating and possibly death if exposed continuously to full sun.

Thermoregulation Indices

The index d_e was determined from T_e data obtained by moving an exoskeleton randomly throughout the environment and T_bs selected in the laboratory thermal gradient. Although the lower limit of T_{sel} was 22.1 °C, T_es at the field site never reached below 23

°C during this study. In addition, because nocturnal temperatures always remained within T_{sel}, d_e is defined as zero and the effectiveness of thermoregulation (E) is undefined for this time period. I thus restricted further analysis to data collected from sunrise to sunset.

During the daytime period, d_b was low (Table 1.3), which indicated that T_bs of active males closely matched T_{sel}, i.e., they seldom experienced temperatures outside the selected T_b range determined in the thermal gradient. The values calculated for d_e during this same period were high, which suggested that the average thermal quality of the habitat (from the animals' perspective) was low, i.e., temperatures were often outside the T_{sel} range. Not surprisingly, E indicated that males thermoregulated carefully (Table 1.3).

However, when I further partitioned the day and analyzed data only from times when tarantulas were active (mornings and evenings) a somewhat different pattern was revealed (Table 1.3). Recalculation of d_b did not change significantly (T_bs closely matched T_{sel}), but the index d_e indicated that in the mornings, the average thermal quality of the habitat was relatively high, i.e., T_e close to T_{sel} (low d_e value) compared to the evenings (high d_e value). As a result, males did not thermoregulate as carefully (E = 0.77) during the morning periods as in the evenings (E = 0.95). T_bs in the evening were close to T_{sel} even though T_es were more often outside T_{sel}.

Emergence and Retreat of Radio-tagged Males

Of the 23 radio-tagged males, three dropped their radio-tags, five were eaten by roadrunners (*Geococcyx californianus*) (personal observation) and one was eaten by a female tarantula after successfully mating with her (successful matings without

cannibalism were also observed on several occasions). I determined that males commenced activity between the hours of 16:36 and 20:53 CST (mean = 19:32 CST). Emergence times before 19:00 occurred only on overcast days.

Once emerged from daytime refuges, males remained active for the entire night. After sunrise, they retreated into new daytime refuges between the hours of 06:47 and 10:53 CST (mean = 08:59 CST). Typical refuges were underground burrows of various size and depths (possibly abandoned rodent burrows). On four occasions when the weather was completely overcast and/or raining for the entire day, males remained above ground and sometimes climbed up on vegetation (trunks of mesquite or tasajillo stems) instead of retreating underground. Air temperatures on these days did not exceed 40°C.

Retreat and emergence times and their associated environmental variables (air and substrate temperatures, relative humidity and light intensity) were analyzed separately (Fig. 1.3). Because tarantula T_bs were not significantly different from either T_a or T_s and usually fell between these two variables, I calculated a mean (T_{env}) of the two that was used in correlation analyses. Trends in linear correlations were similar on day 1 and day 2 so data from both days were pooled.

Linear correlations between emergence and retreat times and the environmental variables are shown in Figure 1.3. If males retreated between sunrise and 10:53 CST and environmental variables did not affect retreat times within that period, then increasing temperature and light levels were expected to be associated positively with time, i.e., a positive correlation. Similarly, humidity levels were expected to decrease with time in the morning (negative correlation). Observation of the retreat data and correlations (Fig. 1.3) suggested that the expected pattern held true; males that stayed active longer in the

morning, experienced hotter and drier conditions with increasing light intensity (T_{env}: $r = 0.98$, $p < 0.01$; light intensity: $r = 0.48$, $p = 0.04$; relative humidity: $r = -0.42$, $p = 0.03$). All but one male found daytime refuges before T_{env} reached above VT_{max} 33°C (mean = 29.4 °C, range = 24.1 – 37.5 °C) and while relative humidity was above 40%.

For evening emergence times, the relationship between humidity and time is a little more complex because around sunset (20:31 CST), humidity starts to rise after reaching daytime lows between 16:00 and 20:00 CST (Fig. 1.4). This time period coincides with emergence of males which explained some of the variability in relative humidity despite the negative correlation ($r = -0.50$, $p = 0.01$) (Fig. 1.3). The expected pattern for temperature and light intensity levels was the reverse of what occurred in the morning (i.e., a negative correlation with time was expected). Time of emergence showed the expected negative correlation with light intensity ($r = -0.57$, $p = 0.01$) as light levels decreased as the sun approached the horizon (~ 20:00 CST) (Fig. 1.3). However, time of emergence did not show the expected negative correlation with T_{env} ($r = 0.22$; $p = 0.21$), suggesting that time of emergence was influenced by temperature, i.e., tarantulas chose to emerge from burrows when temperatures were within some suitable range. This is further supported by the relatively narrow temperature range (29.1 – 38.8 °C) experienced by males when they emerged from their daytime refuges, a range that is relatively independent of time. The upper limit of this range is not too different from VT_{max} (35.1 °C). Only two emergence temperatures were above VT_{max} and these were occurred late in the day, again suggesting that males were waiting for slightly cooler temperatures before emerging from daytime retreats.

To further investigate the influence of temperature on male emergence behavior, I compared emergence times and temperatures on cooler, rainy days versus typically sunny and hot days. On days with continuous heavy cloud cover and intermittent rain, males emerged earlier ($n = 37$, $t = 2.41$; $p = 0.02$) when temperatures were slightly lower ($n = 25$, $t = 2.26$, $p = 0.03$) than on predominantly sunny days (Fig 1.5).

Discussion

Male tarantulas at the CWMA were predominantly nocturnal. During the night thermoregulation was unimportant because environmental temperatures remained within T_{sel} (Shine and Madsen 1996). In comparison, diurnal ranges in temperature, even in the shade, often exceeded T_{sel} and VT_{max} (Fig. 1.2). These patterns of temperature availability can be used to explain temporal activity patterns described for *A. anax* males (e.g., emergence and retreat times) (Grant and Dunham 1988; Hailey and Coulson 1996). In the morning, males typically ceased activity as temperatures approached the upper limit of T_{sel} and before VT_{max} was reached. In the evening, males remained within burrows until temperatures again approached T_{sel} before emerging.

Critical thermal maxima (CTM) of approximately 43 °C (varies slightly with acclimation temperature) have been determined for two species of *Aphonopelma: A. echina* from Texas (Punzo 1991) and *A. chalcodes* from Arizona (Seymour and Vinegar 1973). Although both of these studies described CTM for females only, this is probably a relatively good approximation of CTM for males *(A. anax)* used in this study. Based on this value, daytime temperatures in full sun are probably well beyond the upper critical limits for these animals and even temperatures in the shade (above ground) approached

critical limits. Thus, the thermal environment restricts diurnal locomotory activities by male tarantulas.

Thermoregulation Indices

T_{sel} for these males spanned a relatively wide range of temperatures (Fig. 1.1b) and this variability may simply be a result of the activity of males within the thermal gradient. They avoided the extremes of the gradient (below 20 °C and above 40 °C) but seldom remained in one area of the gradient for more than 20 minutes during the entire 24-hour period. A comparison of males and non-reproductive females or juveniles would be interesting. Because females and juveniles are typically less active than males they may choose to remain within a small area of the gradient which would, in turn, result in a relatively narrow range of T_bs. For mature males, however, locomotor activity is probably more important for mating success that careful body temperature selection, resulting in a broad T_b range. Shine et al (2000) suggest a similar lack of precise body temperature control in male garter snakes (*Thamnophis sirtalis parietalis)* during the mating season.

Calculations of E (effectiveness of thermoregulation) suggested that males thermoregulated more carefully in the evening than in the morning. This suggestion is supported by lack of correlation between evening emergence time and temperature (Fig. 1.3) i.e., temperature apparently influenced the decision of when to emerge. Combining behavioral observations with these data provided further evidence for the influence of temperature on emergence time. Very often males became visible near the entrance of their temporary, daytime burrows up to an hour before they initially emerged, and on

numerous occasions, males emerged and almost immediately returned to the confines of the burrow. This activity was more likely to occur if males emerged well before sunset when T_a and T_s were still relatively high, suggesting that temperature may have influenced this behavior. Thus, effective thermoregulation for these animals was achieved by finding and remaining within a thermally suitable retreat. Once active, however, night-time environmental temperatures were within T_{sel} so there was no need for males to thermoregulate.

In the morning, the thermal quality of the habitat was typically closer to T_{sel} (low d_e value) and areas of partial shade were readily available so males could avoid exposure to full sun relatively easily and remain active. Males appeared to actively avoid exposure to full sun, particularly towards 10:30 am as T_a and T_s increased quickly above T_{sel}. Behaviors included actively retreating from sunny locations and/or increasing their rate of locomotion in sunny areas compared to shaded areas. Despite these behaviors, males appeared to be very particular about the choice of temporary daytime retreats. They often investigated and rejected several burrows before finding a retreat where they would remain throughout the hot part of the day. Because of the clumped nature of the vegetation at the site, rejection of burrows in one clump meant that males often had to cross relatively open, unshaded areas in search of additional burrows. Towards 10 am, these unshaded areas represented thermally stressful habitat (Fig. 1.2).

Emergence and Retreat

Based on observed activity patterns, it appeared that choice of retreat site was a more important cue to determining when males ceased activity than was temperature

because many males retreated into burrows while temperatures were still well within T_{sel}.

Although finding retreat sites during the day may be very important for males to avoid heat stress and desiccation, thermally "suitable" retreats also increase the time spent at physiologically favorable T_bs (Schauble & Grigg 1998; Webb & Shine 1998; Huey et al. 1989). These more favorable T_bs in turn affect physiological traits such as metabolic rates (Huey & Slatkin 1976; Bennett & Nagy 1977; Stevenson 1985; Huey 1991; Peterson et al. 1993). Males that found burrows where temperatures remained well below 40 °C would have T_bs of a similar temperature and so would experience lower daytime metabolic rates (Chapter 2; Punzo 1991), thus minimizing energy expenditures (Huey 1991, Beaupre 1995). This reduced energy expenditure during the day may then translate into more energy available for locomotory mate searching over the entire mating season. In addition, males that found burrows and ceased activity earlier had reduced time of exposure to daytime predators such as roadrunners (personal observation). The costs associated with finding suitable burrows included time spent investigating many different burrows, which reduced time available for mate searching, as well as increased energetic expenditure and thermal stress as tarantulas moved between shrub clumps and were exposed to the sun's radiation. In addition, males that found a suitable retreat early in the morning and ceased activity may have reduced their chances of finding receptive females because of shorter periods of mate searching activity. In the morning, there appeared to be a trade-off between extensive searching for receptive females while temperatures were within appropriate limits, and finding and remaining in suitable burrows.

Minch (1978) and Punzo and Henderson (1999) reported that light intensity influences activity of female tarantulas. In addition, under conditions of low relative humidity, Punzo (1991) suggested that tarantulas (both males and females) are less resistant to temperature stress. At CWMA, percent relative humidity usually remained above 80% at night and started to decrease slowly with daybreak (Fig. 1.4). During morning activity periods of males, values typically remained above 60%. At times of emergence, relative humidity was often in the 20-40 % range. Thus, it appears that, for short periods, *A. anax* can tolerate relatively low humidity.

Although my data suggested that temperature was the most limiting factor on male tarantula activity, I observed exceptions to this on several days when daytime temperatures remained in the high 30's throughout the day due to heavy cloud cover. Despite these moderate temperatures, males were still inactive during the middle part of the day. As a result, the influences of light intensity and humidity need to be examined in more detail. A comparison between tropical rainforest species and desert species would be interesting both in terms of rates of water loss and times of activity. Stradling (1994) observed arboreal tarantulas *(Avicularia avicularia)* in Trinidad where temperatures were generally moderate and there was an extended rainy season during which males were active. Most of his observations were of females. Despite cooler and wetter temperatures, these animals were predominantly nocturnal. Unfortunately, Stradling (1994) did not report on activity times for males.

Cloudsley-Thompson (1991) suggested that in desert ectotherms, emergence and retreat times are controlled by a combination of responses to environmental factors and circadian rhythm or biological clocks. Even under controlled laboratory conditions,

many desert animals exhibit strong circadian rhythms of locomotory activity (Cloudsley-Thompson 1991). Although CWMA is not considered a desert environment, the hot and arid conditions are more typical of a desert than tropical and/or temperate environments. Surprisingly, in the laboratory thermal gradient, movement and corresponding T_bs of males appeared completely random for all males throughout the 24-hour period and showed no discernible patterns. In a laboratory study of metabolic rates of this same species (Chapter 2), I also did not find any nocturnal/diurnal patterns (measured as increased metabolic rates) over a 24-hour period that might have corresponded to a circadian rhythm.

Finally, in a comparison of locomotory activity in tropical and desert arachnids, Cloudsley-Thompson (1981) suggested that tropical and woodland species of tarantulas were less active than desert forms and the former were more likely influenced by thermal fluctuations. Alternatively, desert tarantulas were influenced most strongly by light and dark cycles. However, his study used females that had been in captivity for an undetermined period, so it is uncertain how these results would compare with field-active animals. It would be interesting to compare life history variation between mature males from different climates because locomotory activity is linked to the thermal environment and is also a key determinant to mating success for most (all?) species.

Activity of male tarantulas during the mating season appears to be influenced by a combination of thermal and energetic considerations. The behavior of ectotherms under different thermal conditions may vary widely and as a result there may be differences in performance capabilities among individuals (Willmer 1991; Adolph and Porter 1993). Where mating behavior patterns are involved, differences may influence an individual's

fitness. Unfortunately, at the CWMA field site it was very difficult to find female burrows because they were typically well-hidden under thick, thorny shrubs (although I have been relatively successful at finding burrows at other sites). This made it difficult to correlate male activity with actual mate acquisition; this would make an interesting study in the future.

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References

Adolph, S. C. and Porter, W.P. 1993. Temperature, activity, and lizard life histories. Am. Nat., **142**: 273-295.

Avery, R. A. 1982. Field studies of body temperatures. *In* Biology of the reptilia, vol. 12. *Edited by* C. Gans and F. H. Pough. Academic Press, New York. pp. 68-91.

Baerg, W. J. 1958. The tarantula. University of Kansas Press. Lawrence.

Bakken, G.S. 1981. A two-dimensional operative-temperature model for thermal energy management by animals. J. Therm. Biol., **6**: 23-30.

Bakken, G. S. 1992. Measurement and application of operative and standard operative temperatures in ecology. Amer. Zool., **32**: 194-216.

Bauwens, D., P. Hertz and A. M. Castilla. 1996. Thermoregulation in a lacertid lizard: the relative contribution of distinct behavioral mechanisms. Ecology, **77**: 1818-1830.

Beaupre, S. J. 1995. Effects of geographically variable thermal environments on bioenergetics of mottled rock rattlesnakes. Ecology, **76**: 1655-1665.

Bennett, A.F., and Nagy, K.A. 1977. Energy expenditure in free-ranging lizards. Ecology, 58: 697-700.

Carrel, J. E. (1978): Behavioral thermoregulation during winter in an orb-weaving spider. Symposium of the Zoological Society of London **42**: 41-50

Casey, T. M. 1981. Behavioral mechanisms of thermoregulation. *In* Insect thermoregulation. *Edited br* B. Heinrich. John Wiley & Sons, New York. pp. 79-109.

Casey, T. M. 1992. Biophysical ecology and heat exchange in insects. Am. Zool., **32**: 225-237.

Chew, R. M. 1961. Ecology of the spiders of a desert community. Jl. N.Y. Ent. Soc., **69**: 5-41.

Chappell, M. A. 1983. Metabolism and thermoregulation in desert and montane grasshoppers. Oecologia, **56**: 126-131

Cloudsley-Thompson, J. L. 1981. A comparison of rhythmic locomotory activity in tropical forest Arthropoda with that in desert species. J. arid Environs., **4**: 327-334.

Cloudsley-Thompson, J. L. 1991. Ecophysiology of desert arthropods and reptiles. Springer-Verlag, Berlin.

Cloudsley-Thompson, J. L. 1993. Ecophysiology of desert arachnida. Boll. Acc. Gioenia Sci. Nat., **26**: 53-63.

Davies, M. E. and Edney, E. B. (1952). The evaporation of water from spiders. J. exp. Biol., **29**: 571-582.

Diaz, J.A. 1994. Ecological correlates of the thermal quality of an ectotherm's habitat: a comparison between two lizard populations. Func. Ecol., **11**: 79-89.

Grant, B. W. and Dunham, A.E. 1988. Thermally imposed time constraints on the activity of the desert lizard *Sceloporus merriami*. Ecology, **69**: 167-176.

Hailey, A. and Coulson, I.M. 1996. Temperature and the tropical tortoise *Kinixys spekii*: constraints on activity level and body temperature. J. Zool. Lond., **240**: 523-536.

Hammerstein, P. and Reichert, S.E. 1988. Payoffs and strategies in territorial contests: ESS analyses of two ecotypes of the spider *Agelenopsis aperta*. Evol. Ecol., **2**: 115-138.

Heinrich, B. 1981. Insect thermoregulation, vol. 1. John Wiley and Sons, New York.

Hellgren, E. C., Kazmaier, R. T., Ruthven, D. C. and Synatzske, D. R. (2000). Variation in tortoise life history: demography of *Gopherus berlandieri*. Ecology, **81,** 1297-1310.

Hertz, P. E. 1992. Temperature regulation in Puerto Rican *Anolis cookis* and *A. cristatellus*: a field test using null hypotheses. Ecology, **73**: 1405-1417.

Hertz, P. E., Huey, R. B. & Stevenson, R. D. 1993. Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. Am. Nat., **145**: 796-818.

Huey, R. B. 1982. Temperature, physiology, and the ecology of reptiles. *In* Biology of the reptilia, vol 12. *Edited by* C. Gans and F. H. Pough. Academic Press, New York. pp. 25-91.

Huey, R. B. 1991. Physiological consequences of habitat selection. Am. Nat., **137**: 91-115.

Huey, R. B., Peterson, Arnold, S.J. and Porter, W.P. 1989. Hot rocks and not-so-hot rocks: retreat-site selection by garter snakes and its thermal consequences. Ecology, **70**: 931-944.

Huey, R. B. and Slatkin, M. 1976. Cost and benefits of thermoregulation. Quart. Rev. Biol., **51**: 363-384.

Humphreys, W. F. 1974. Behavioural thermoregulation in a wolf spider. Nature, **251**: 502-503.

Humphreys, W. F. 1978. The thermal biology of *Geolycosa godeffroyi* and other burrow inhabiting Lycosidae (Araneae) in Australia. Oecologia, **31**: 319-347.

Humphreys, W. F. 1987. Behavioural Temperature Regulation. *In* Ecophysiology of spiders. *Edited by* W. Nentwig. Springer-Verlag, Berlin. pp. 56-65.

Janowski-Bell, M. E. and Horner, N. V. 1999. Movement of the male brown tarantula, *Aphonopelma hentzi* (Araneae: Theraphosidae), using radio telemetry. Journal of Arachnology, **27**: 503-512.

Kearney, M. and Predavec, M. 2000. Do nocturnal ectotherms thermoregulatate? A study of the temperate gecko *Christinus marmoratus.* Ecology, **81**: 2984-2996.

Kingsolver, J. G. 1989. Weather and the population dynamics of insects: integrating physiological and population ecology. Physiol. Zool. **62**: 314-334.

Lubin, Y. D. and Henschel, J. R. 1990. Foraging at the thermal limit: burrowing spiders *(Seothyra Eresidae)* in the Namid desert dunes. Oecologia, **84**: 461-467.

Minch, E. W. 1978. Daily activity patterns in the tarantula *Aphonopelma chalcodes* Chamberlin. Bull. Brit. Arachnol. Soc., 4: 231-237.

Peterson, C. R. 1987. Daily variation in the body temperature of free-ranging garter snakes. Ecology, **68**: 160-169.

Peterson, C. R., Gibson, A. R. & Dorcas, M. E. (1993). Snake thermal ecology: the causes and consequences of body-temperature variation. *In* Snakes ecology and behavior. *Edited by* R. A. Seigel and J. T. Collins. McGraw-Hill, Inc., New York. pp. 241-314.

Porter, W.P. and Gates, D.M. Thermodynamic equilibria of animals with environment. Ecol. Mon., 29: 227-244.

Pulz, R. 1987. Thermal and water relations. *In* Ecophysiology of Spiders. *Edited by* W. Nentwig. Springer-Verlag, Berlin. pp. 26-55.

Punzo, F. 1991. Intraspecific variation in responses to thermal stress in the tarantula, *Dugesiella echina* Chamberlin (Orthognatha: Theraphosidae). Bull. Brit. Arachnol. Soc., **8**: 277-283.

Punzo, F., and Henderson, L. (1999): Aspects of the natural history and behavioral ecology of the tarantula, Aphonopelma hentzi (Girard 1854) (Orthognatha:

Theraphosidae). Bull. Brit. Arachnol. Soc., **11**: 121-128.

Punzo, F., and Jellies, J. 1983. Comparative water relations of araneid and lycosid spiderlings. Comp. Biochem. Physiol., **74A**: 981-988.

Riechert, S.E. 1981. Games spiders play. II. Resource assessment strategies. Behav. Ecol. and Sociobiol., **6**: 121-128.

Riechert, S.E. 1985. Decisions in multiple goal contexts: habitat selection of the spider, *Agelenopsis aperta* (Gertsch). Zeitschrift fur Tierpsychologie, **70**: 53-69.

Riechert, S.E. and Tracy, C.R. 1975. Thermal balance and prey availability: bases for a model relating web-site characteristics to spider reproductive success. Ecology **56**: 265-284.

Rummery, C., Shine, R., Houston D.L., and Thompson, M.B. 1994. Thermal biology of the Australian forest dragon, *Hypsilurus spinipes* (Agamidae). Copeia, **1994**: 818-827.

Schauble, C. S. and Grigg, G.C. 1998. Thermal ecology of the Australian agamid *Pogona barbata*. Oecologia, **114**: 461-470.

Seymour, R. S. and Vinegar, A. 1973. Thermal relations, water loss and oxygen consumption of a North American tarantula. Comp. Biochem. Physiol., **44A**: 83-96.

Shillington, C., and Verrell, P. 1997. Sexual strategies of a North American 'tarantula' (Araneae: Theraphosidae). Ethology, **103**: 588-598.

Shine, R., Harlow, P.S., Elphick, M.J., Olsson, M.M., and Mason, R.T. 2000. Conflicts between courtship and thermoregulation: the thermal ecology of amorous male garter snakes (*Thamnophis sirtalis parietalis,* Colubridae). Physio. Biochem. Zool., **73**: 508-516.

Shine, R. and Madsen, T. 1996. Is thermoregulation unimportant for most reptiles? An example using water pythons *(Liasis fuscus)* in tropical Australia. Physiol. Zool., **69**: 252-269.

Stevenson, R. D. 1985. Body size and limits to the daily range of body temperatures in terrestrial ectotherms. Am. Nat., **125**: 102-117

Stradling, D.J. 1994. Distribution and behavioral ecology of an arboreal "tarantula" spider in Trinidad. Biotropica, **26**: 84-97.

Thornhill, R. and Alcock, J. 1983. The evolution of insect mating systems. Harvard University Press, Cambridge.

Webb, J.K. and Shine, R. 1998. Thermoregulation by a nocturnal elapid snake *(Hoplocephalus bungariodes)* in southeastern Australia. Physiol. Zool., **71**: 680-692.

Warburg, M.R. and Polis, G.A 1990. Behavioral responses, rhythms and activity patterns. *In* The biology of scorpions. *Edited by* G.A. Polis. Stanford University Press, Stanford. pp 224-246.

Willmer, P. (1991). Thermal biology and mate acquisition in ectotherms. TREE., **6**: 396-399.

Table 1.1: Body and leg sizes of male and female tarantulas (*Aphonopelma anax*).

	Females mean ± SE	**Males mean ± SE**	**t**	**P**
Mass (g)	13.75 ± 2.37	8.31 ± 0.29	4.39	<0.01
Carapace Length (mm)	17.84 ± 0.79	17.81 ± 0.26	0.03	0.96
Carapace Width (mm)	21.12 ± 1.58	18.34 ± 0.3	2.8	<0.01
Abdomen Length (mm)	23.17 ± 1.99	18.50 ± 0.29	4.48	<0.01
Leg 1 (mm)	52.51 ± 2.81	62.43 ± 0.77	3.40	0.02
Leg 2 (mm)	49.33 ± 2.58	60.54 ± 0.72	4.19	< 0.01
Leg 3 (mm)	46.98 ± 2.50	58.10 ± 0.74	4.27	< 0.01
Leg 4 (mm)	55.10 ± 2.63	70.70 ± 1.13	5.45	< 0.01

Table 1.2: Diurnal operative temperatures in different microhabitats compared with laboratory selected T_bs and field measured T_bs of active males.

	Mean Temperature (°C) ± S.E.	**Range of Temperatures (°C)**
T_e sun	41.7 ± 0.9	23.9 - 63.2
T_e shade	32.3 ± 0.3	23.6 – 46.8
T_e random	43.1 ± 0.7	23.9 – 71.6
T_{burrow}	32.9 ± 0.3	27.5 – 37.4
T_b in laboratory thermal gradient	27.6 ± 0.2	18.0 – 35.3
T_{sel}	27.4 ± 0.2	22.1 – 31.3
Field measured T_bs	29.4 ± 0.5	24.7 – 35.1

Table 1.3: Mean body temperature (T_b) of active male tarantulas, operative temperatures (T_e), and indices of thermoregulation separated into daytime and nighttime hours. Within each day, the hours are further broken down into morning and evening activity periods (d_b = mean deviation of body temperatures from selected body temperature; d_e = mean deviation of operative temperatures from selected body temperatures; E = effectiveness of thermoregulation.

	T_b (°C)	T_e (°C)	d_b	d_e	E*
DAY					
(6:43-20:41)	29.8 ± 0.7	43.4 ± 0.7	0.55 ± 0.2	12.51 ± 0.6	0.96
morning (6:43-10:53)	28.79 ± 1.5	29.7 ± 0.6	0.98 ± 0.6	4.11 ± 0.5	0.77
evening (16:36-20:41)	30.29 ± 0.7	35.8 ± 0.8	0.42 ± 0.2	8.84 ± 0.9	0.95
NIGHT					
(20:42-6:42)	29.4 ± 0.3	26.1 ± 0.1	0.87 ± 0.1	0	-

* $E = 1 - d_b / d_e$ and varies between 0 and 1 (0 = no thermoregulation, 1 = precise thermoregulation)

List of Figures

Figure 1.5: Emergence times and temperatures of male tarantulas on days with continuous heavy cloud cover and intermittent rain, compared with typically sunny and hot days.

FIGURE 1.1: Comparison of T_bs and T_e.

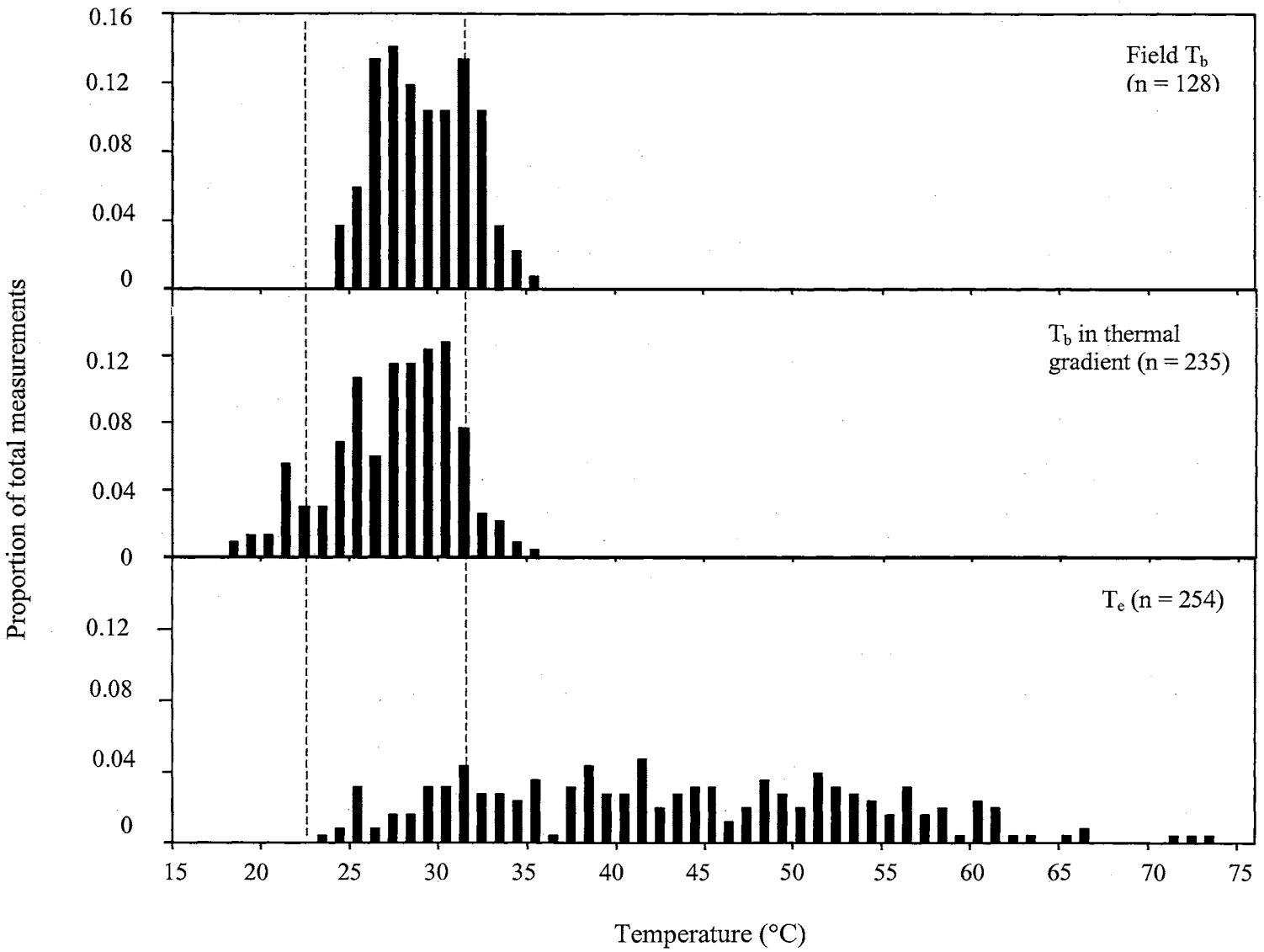


FIGURE 1.2 Comparison of T_es

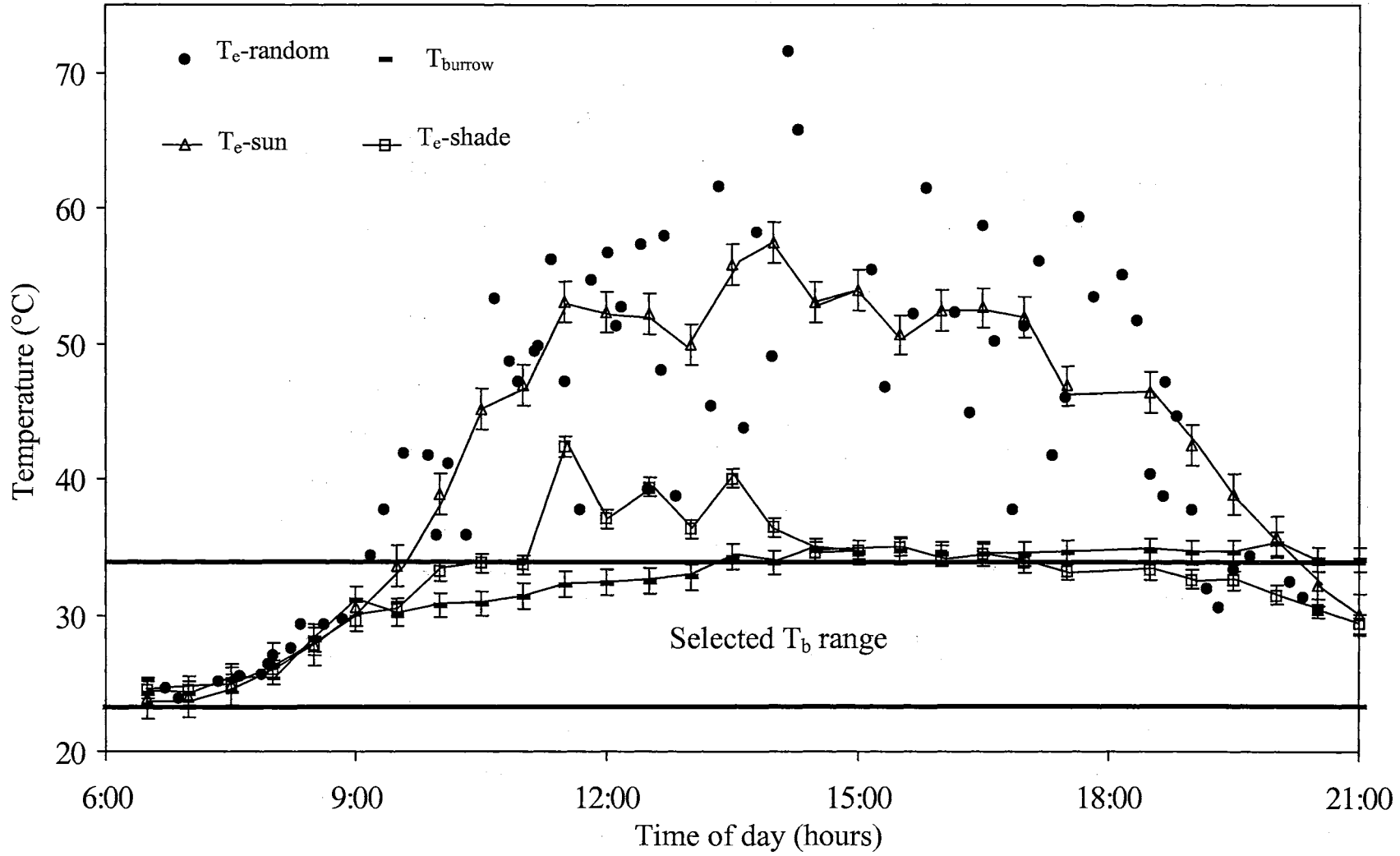


FIGURE 1.3: Emerge and Retreat

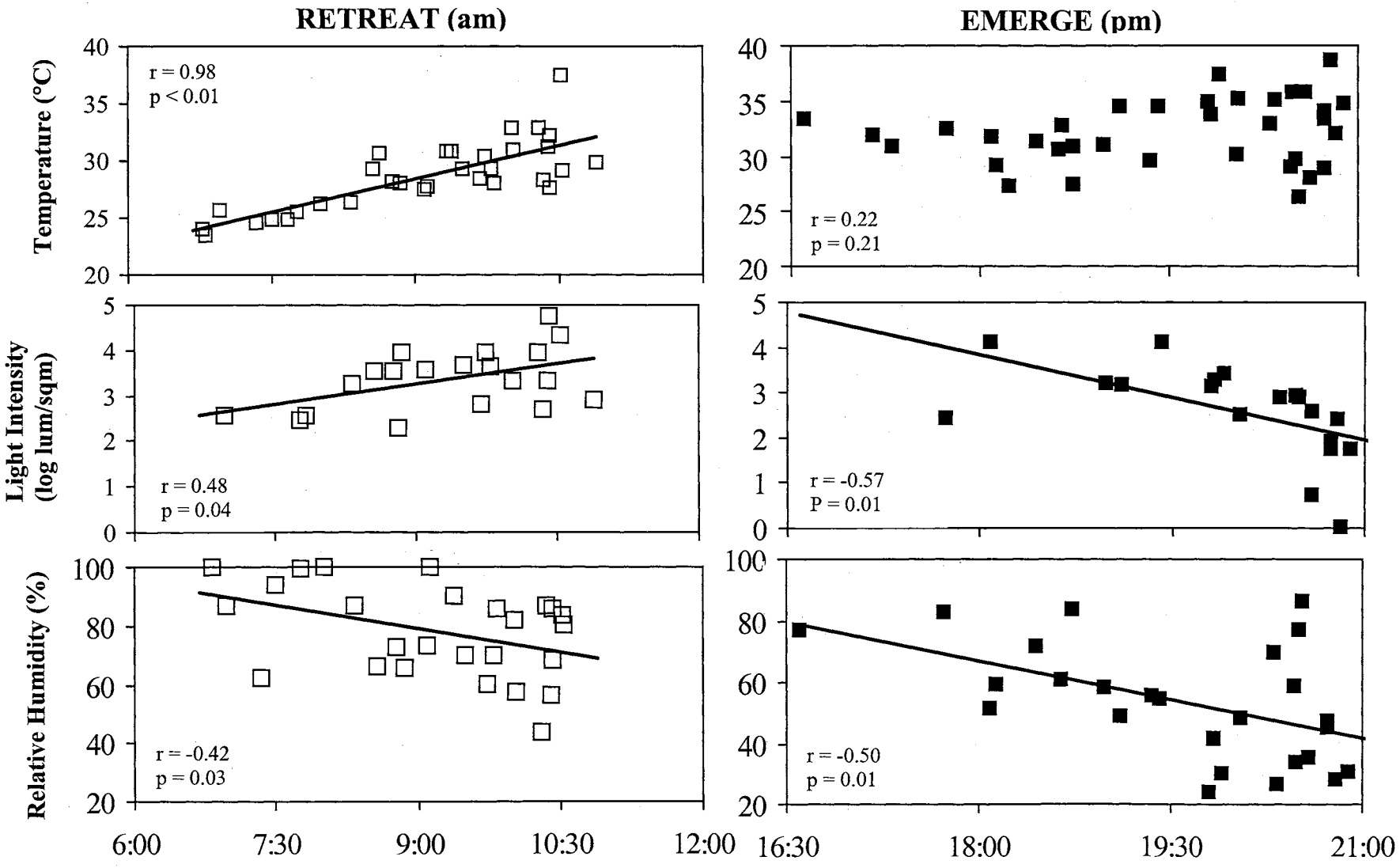


FIGURE 1.4: Relative Humidity over a 24 hour period.

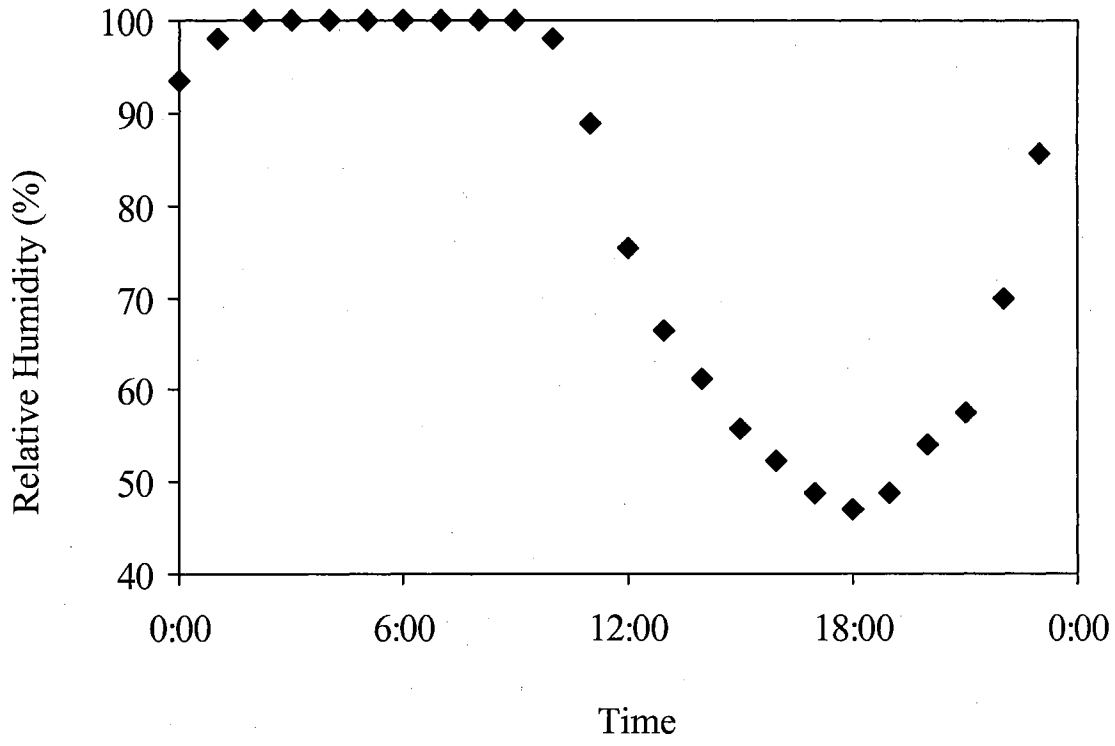
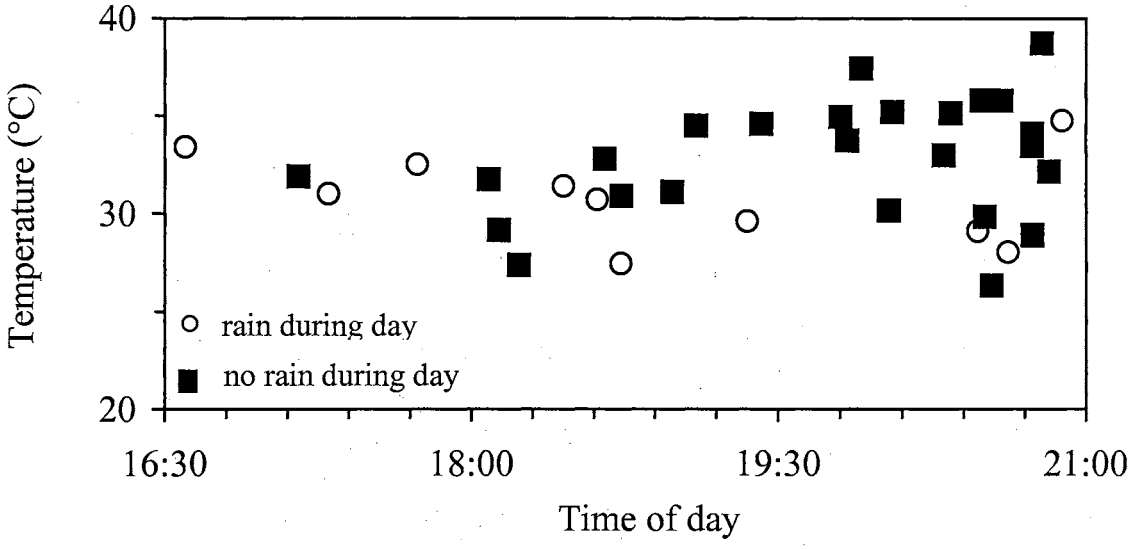


FIGURE 1.5: Retreat on sunny and rainy days.



CHAPTER 2

SEXUAL DIMORPHISM IN RESTING METABOLIC RATE AND EVAPORATIVE WATER LOSS IN THE TEXAS TARANTULA, APHONOPELMA ANAX

Abstract – In animals, physiological traits such as rates of metabolism and evaporative water loss are dependent on body temperature. I measured rates of resting metabolism and evaporative water loss in male and female tarantulas (Aphonopelma anax) and tested for the effects of body mass, temperature and sex.

Resting metabolic rates (RMRs) were measured as rates of CO_2 production ($\dot{V}_{CO_2}$) in an open-flow respirometry system at 20, 25, 30 and 35 °C. Evaporative water loss (EWL) was measured simultaneously using Drierite-filled water traps. Mass-scaling equations were determined for both RMR and EWL. An RQ of 0.92 was calculated from rates of CO_2 production and O_2 consumption in a closed, constant-volume respirometry system. This RQ was used to convert $\dot{V}_{CO_2}$ to $\dot{V}_{O_2}$ to compare my data with available literature on metabolic rates. RMRs increased with increasing temperature. In addition, at each temperature males had substantially higher metabolic rates than females after adjusting for the influence of body mass. Evaporative water loss was similar between males and females at lower temperatures, but differences between the sexes were substantial at 35 °C. The index of water use effectiveness (E) comparing the ratio of EWL to RMR in individual animals, indicated that at high temperatures, water conservation in males was more effective than in females.

Introduction

The total energy available to animals is limited by resource abundance, thermal constraints on foraging time (especially among ectotherms), and physiological rates of food processing. Thus, variation in energy expenditure, which is strongly influenced both by environmental factors such as temperature and time of day, and by intrinsic factors such as body mass or sex (Bennett and Dawson 1976; Beaupre 1993; Beaupre et al. 1993), may in turn influence net energy allocation to growth, storage, and reproduction. Differences in these allocations within and among individuals may then affect behavior, life history, and population dynamics (Dunham et al. 1989; Beaupre and Duvall 1998).

Sex differences in resting metabolic rates (RMRs) have been studied in various animals, with mixed results. Among invertebrates, differences have been found in some taxa but not others (true bugs: Hebbalkar and Sharma 1991; millipedes: Penteado and Hebling-Beraldo 1991; spiders: Humphries 1977; Kotiaho 1998). Sexual differences in basal metabolic rates are common in birds, but the direction and magnitude of these differences are variable (Rintamaki et al. 1984; Kaiser and Bucher 1985; Maloney and Dawson 1993). The same is true for reptiles (Bennett and Dawson 1976; Jameson, et al. 1976; Beaupre 1993; Beaupre et al. 1993; Beaupre and Duvall 1998; Cullum 1998). Some of the sexual dimorphism in metabolic rates can be explained by size differences between males and females, reproductive condition, and proportions of different tissue types (Sanborn and Jankowski 1994; Beaupre and Duvall 1998; Cullum 1998).

Spiders exhibit much variability in rates of energy expenditure and, as with most organisms, body size accounts for most of this variation (Anderson 1970; Greenstone and

Bennett 1980). Low rates of energy expenditure may be adaptive in an unstable environment where there may be periods of reduced prey availability (Seymour and Vinegar 1973; Greenstone and Bennett 1980; Anderson 1994). This idea is supported in comparative studies of the metabolic rates of comb-footed spiders (Anderson 1994) and ticks (Lighton and Fielden 1995). Higher rates of metabolism found in most orb-weavers and comb-footed spiders is associated with higher growth rates and larger clutch sizes (Greenstone and Bennett 1980; Anderson and Prestwich 1982; Anderson 1994). As a group, however, most spiders demonstrate low rates of metabolism compared to other arthropods of similar size (Anderson 1970; Anderson and Prestwich 1985; Anderson 1996).

Selection pressures associated with energetic demands are different for male and female spiders. After reaching sexual maturity, most males change their habits and leave their retreats or webs to search actively for females (Foelix 1996). Males are relatively short-lived and the energy used in gamete production is small, though costs of locomotion may be high. Females maintain a larger body size over a longer life span and also have a higher energetic cost associated with gamete production and, in some species, parental care (Foelix 1996).

Male tarantulas (Theraphosidae: Aphonopelma) of North America engage in intense mate-searching activity during the summer mating season. They engage in scramble competition (Shillington and Verrell 1997) for opportunities to mate and their mating success depends largely on rapid walking. As a result, adult male tarantulas have higher energy life styles than females. Several recent studies have suggested that animals with high metabolic rates in the field often also have high RMRs (Daan et al. 1990;

Koteja 1991; Ricklefs and Miles 1994; Reinhold 1999; Rogowitz and Chappell 2000).

During times of activity during the mating season, male tarantulas are exposed to greater fluctuations in environmental temperatures and are more susceptible to dehydration than females, due to exceedingly high daytime temperatures and low relative humidity (Chapter 1). Evaporative water loss (EWL) in arthropods occurs via cuticular transpiration and evaporation from respiratory surfaces (Pulz 1983, 1987; Cloudsley-Thompson 1991). Water is a major component of spiders (body fluids are 60-85 % water: Pulz 1987) and these body fluids provide hydrostatic pressure for locomotion (Foelix 1996).

Based on differences in life history traits of adult male and female tarantulas leading to higher energy demands for males, I predicted that male tarantulas would have higher resting metabolic rates (RMRs) than females. Because of higher RMRs, obligate EWL associated with respiratory transpiration is likely to be higher in males compared to females. However, because of the importance of maintaining a hydrostatic skeleton for locomotion, and the need for prolonged locomotion in mate searching activities for male tarantulas, I predicted that selection for water conservation may be stronger in males than females. Thus, although EWL due to respiration may be higher in males, they may compensate by having reduced EWL across the cuticle. In this study I compared RMRs and EWL of male and female tarantulas (Aphonopelma anax) from Texas. In the context of natural and sexual selection, these whole animal traits are of interest because they represent integrated features of an animal's physiology that interact directly with environmental factors and can influence ecological variables such as activity times, reproductive tactics and population dynamics.

Materials and Methods

Study Animals

During May-July of 1999 and 2000, I collected male and female tarantulas at the Chaparral Wildlife Management Area (CWMA), which is approximately 13 km west of Artesia Wells, TX. This 6.150-ha area is managed by the Texas Parks and Wildlife Department. Animals were transported to Oklahoma State University and maintained in the laboratory in individual 3.8-liter containers under a natural photoperiod (14:10 light:dark) and at a room temperature of 20-28 °C. Water was constantly available and food (crickets and occasionally mealworms) was available ad libitum except during the week prior to metabolic measurements.

Resting Metabolic Rates

I used an open-flow respirometry system to measure rates of CO_2 production ($\dot{V}_{CO_2}$) of animals during rest. Outside air was drawn at a flow rate of 100 ml/min (Sierra mass flow controller). This air initially passed through a Drierite/Ascarite/Drierite column to remove both CO_2 and water from the air before passing into animal chambers and finally through a LiCor 6251 CO_2 analyzer. The CO_2 analyzer was interfaced with a computer running analog-to-digital data acquisition software (Sable System, Salt Lake City, Utah). Eight chambers were available for simultaneous measurements. I measured metabolic rates of seven tarantulas concurrently with one chamber empty for a baseline reference. Each chamber had a volume of 235 ml. Occupied chambers were sampled for 25 minutes sequentially. Both before and after

sampling the occupied chambers, the unoccupied chamber was sampled for 7.5 minutes to provide two baseline recordings. The total recording time for all 8 chambers was therefore 190 minutes. When not being sampled, chambers were flushed with dry, CO_2-free air.

For each animal, RMRs were measured at 20, 25, 30 and 35 °C and the order of temperatures was randomized. These experimental temperatures spanned the range of body temperatures measured in active male tarantulas at the field site (Chapter 1). To maintain these temperatures, the animal chambers were housed in an environmental chamber set at the appropriate temperature. The environmental chamber also maintained the same natural photoperiod. At the lower three temperatures (20, 25, 30 °C), RMRs were measured over a 24-hour period (approximately eight recordings per animal per temperature). At 35 °C, RMRs were recorded only twice for each animal to reduce exposure to high temperatures for a total time of approximately six hours. $\dot{V}_{CO_2}$ was calculated from fractional concentrations of CO_2 entering (Fi) and leaving (Fe) the respirometry chambers using the equation from Withers (1977):

$$\dot{V}_{CO_2}\ (\text{ml/h}) = (Fe_{CO_2} - Fi_{CO_2}) * (\text{flow rate in ml h}^{-1})$$

Fi was zero because incoming air was scrubbed of CO_2 using Ascarite. RMRs were determined as the mean of the lowest five minutes of steady-state $\dot{V}_{CO_2}$ during each 25-minute recording period.

To determine if there were nocturnal/diurnal cycles in RMRs (related to activity in the animal chambers), the 24-hour RMR measurements were divided into periods of activity and inactivity based on field observations, i.e., 06:30 – 11:00 (diurnal 1/active),

11:00 – 18:30 (diurnal/inactive), 18:30 - 20:30 (diurnal 2/active), and 20:30 – 06:30 (nocturnal/active).

To linearize the relationship between $\dot{V}_{CO_2}$ and body mass prior to analysis of RMRs, these two variables were $\log_{10}$ transformed. Additionally, because of the confounding effects of body mass on metabolic rate (i.e., $\dot{V}_{CO_2}$ increases with increasing body mass), I used residuals from the allometric regression line (all temperatures and all individuals combined) as a mass-corrected RMR response variable in further analyses to determine the effects of temperature, sex and year on RMRs. The slopes of $\log_{10} \dot{V}_{CO_2}$ and $\log_{10}$ body mass (at each temperature and between males and females) were tested for heterogeneity before analyzing the residuals with repeated-measures analysis of variance (ANOVA).

To compare my results with representative arthropods, I computed mass scaling equations using $\dot{V}_{CO_2}$ and also converted $\dot{V}_{CO_2}$ to rates of oxygen consumption ($\dot{V}_{O_2}$) and to metabolic rates in microwatts (μW). These conversions were based on measures of the respiratory quotient of relatively inactive males and females (see section below) and Joule-CO_2 coefficients (for (μW) (Nagy and Gessman 1988). I used least-squares regression to construct predictive allometric equations for metabolic rates (in ml CO_2 h^{-1} and in μW) as a function of body mass. An equation in the form $\log_{10} \dot{V}_{CO_2} = X_1 * \log_{10} M + y_0$ (where $\dot{V}_{CO_2}$ is in ml h^{-1}; X_1 and y_0 are the slope and y-intercept respectively; M is body mass in g) can then be converted into the general form $\dot{V}_{CO_2}$ (ml h^{-1}) = a M^b.

Respiratory Quotient (RQ)

RQ was calculated as the ratio of $\dot{V}_{CO_2}$ to $\dot{V}_{O_2}$ in a closed, constant-volume respirometry system. This constant-volume technique was necessary because $\dot{V}_{O_2}$ data were unreliable with flow-through respirometry due to low flow rates necessary to optimize the CO_2 signal. Animals were placed in 235-ml containers each fitted with two stopcocks. One hour prior to starting each trial, these containers were placed in the environmental chamber at 25 °C. After an hour, containers were removed from the environmental chamber and a 10-ml air sample was collected from each animal chamber with a plastic syringe fitted with a stopcock. To ensure adequate mixing of the air sample, the syringe was pumped several times before drawing and sealing the syringe stopcock. The stopcocks on the animal chambers were then closed and the time was noted. Sealed animal chambers were then returned to the 25 °C environmental chamber where they were left undisturbed for approximately four hours. After this period, another 10-ml air sample was drawn from the animal chambers.

O_2 and CO_2 content of the 10-ml samples were determined with a Sable Systems FC-1 oxygen analyzer and a LiCor 6251 CO_2 analyzer connected in series. As described above with the CO_2 analyzer, outside air was drawn at a flow rate of 100 ml/min (Sierra mass flow controller) through a Drierite/Ascarite/Drierite column and then into the two analyzers. The O_2 analyzer was interfaced with the same computer running an analog-to-digital data acquisition software (Sable System, Salt Lake City, Utah). Both initial and final air samples for each animal were injected into a length of Tygon tubing just prior to a Drierite/Ascarite/Drierite column and O_2 and CO_2 contents were calculated by

integrating fractional concentration over time and multiplying by flow rate (Peterson 1990). $\dot{V}_{CO_2}$ and $\dot{V}_{O_2}$ were calculated as:

$$\dot{V}_{CO_2} \text{ (ml } CO_2 \text{ h}^{-1}) = V_a * (V_b / 10 \text{ ml}) * t^{-1}$$

$$\dot{V}_{O_2} \text{ (ml } O_2 \text{ h}^{-1}) = V_c * (V_b / 10 \text{ ml}) * t^{-1}$$

where V_a was the volume of carbon dioxide increase in the 10 ml air samples (determined from the difference between initial and final air samples), and similarly V_c was the volume of oxygen depleted from the 10 ml air samples. V_b in both equations was the effective volume of the sealed chamber (235 ml – volume of animal). The volume of an animal was estimated as 1.01 * body mass. Finally, t was the elapsed time in hours.

Evaporative Water Loss

During summer 2000, evaporative water loss (EWL) was measured simultaneously with RMR at each temperature. EWL was measured over a 24-hour period at 20, 25 and 30 °C and for approximately 6 hours at 35 °C. Water traps consisted of two 3-ml plastic syringes connected in series and filled with Drierite. To start EWL measurements, airflow to individual chambers (including the empty baseline chamber) was interrupted and pre-weighed water traps were added to the flow line exiting the chambers. At the end of the entire recording period, water traps were removed and weighed and elapsed time was calculated. After adjusting the mass of the water traps by subtracting apparent water loss from the empty chamber (to control for potential small leaks in the system), EWL was considered to be equal to the increase in mass of the water traps during the recording period (g h^{-1}).

Again, EWL and body mass were $\log_{10}$ transformed to linearize the relationship between these variables. To correct for confounding effects of body mass, I used the residuals from the regression line of log-transformed EWL and body mass as a mass-corrected response variable. The slopes of $\log_{10}$ EWL and $\log_{10}$ body mass (at each temperature and between males and females) were tested for heterogeneity before analyzing the residuals with repeated-measures analysis of variance (ANOVA). In addition, I used least-squares regression to construct predictive allometric equations for EWL (in g h^{-1}) as a function of body mass.

Respiratory Water Economy

The ratio of EWL to RMR was computed and compared between temperatures and sexes. This ratio can be considered an index of effectiveness of water conservation (E) for individual animals, i.e., g H_2O / ml CO_2. Because E did not scale consistently with body mass, it was calculated from unadjusted EWL and RMR data. A high E would indicate greater loss during respiration compared to a low E, thus suggesting poorer water conservation. This ratio is analogous to the field-based water economy index of Nagy and Peterson (1988).

Results

Resting Metabolic Rates

Fifty-one male tarantulas and 14 females were used in this laboratory study. RMRs varied randomly with time and did not show any nocturnal/diurnal cycle or any other predictable pattern at any of the lower three temperatures ($F_{6,151}$ =1.52, P = 0.17). As a

result, I used the lowest RMR for each individual at each temperature (irrespective of time) in further analyses. At each temperature some metabolic rate measurements were excluded because I was unable to obtain a 5-minute, minimal steady-state $\dot{V}_{CO_2}$. This was more often the case with males than females because males tend to be very active during the mating season even when confined to a small container.

Comparison of raw (before log transformation or mass correction) RMRs of males and females showed that rates of CO_2 production were fairly similar at each temperature, however females were significantly heavier than males ($\underline{t} = 0.03$, $\underline{P} < 0.001$) (Table 2.1). After log transformation of the data, plotting $\dot{V}_{CO_2}$ versus body mass indicated that females typically had lower RMRs than males of similar mass (e.g., Fig. 2.1). These results were similar at 20, 30 and 35 °C. For both males and females, slopes were homogeneous across all temperatures (males: $\underline{F}_{3, 149} = 0.91$, $\underline{P} = 0.44$; females: $\underline{F}_{3, 39} = 0.82$, $\underline{P} = 0.49$). In addition, slopes of log-transformed RMR versus body mass (for all temperatures combined) were homogeneous between the sexes ($\underline{F}_{1,200} = 0.45$, $\underline{P} = 0.50$) and at each temperature slopes were homogeneous between the sexes (20 °C: $\underline{F}_{1,53} = 0.21$, $\underline{P} = 0.65$; 25 °C: $\underline{F}_{1,44} = 3.81$, $\underline{P} = 0.09$; $\underline{F}_{1,49} = 0.48$, $\underline{P} = 0.49$; $\underline{F}_{1,45} = 1.32$, $\underline{P} = 0.26$). However, observation of mass-scaling coefficients indicated that both intercepts and slopes were highly variable among females but were very consistent among males with a sample size almost 4-fold greater than females (Table 2.1).

Results from repeated-measures ANOVA using the mass-corrected response variable (i.e., residuals of $\log_{10} \dot{V}_{CO_2}$ and $\log_{10}$ body mass for all individuals at all

temperatures) are shown in Table 2.2. The overall scaling equation (incorporating both sexes and temperatures) from which these residuals were calculated was:

$\dot{V}_{CO_2} = 0.40 * \log_{10} M - 1.03$ (where M is body mass in grams). $\dot{V}_{CO_2}$ increased with increasing temperature and, at each temperature, the residuals of $\log_{10} \dot{V}_{CO_2}$ were consistently higher for males than females (Fig. 2.2). In addition, the three-way interaction of temperature, sex and year influenced RMR. Examination of temperature by year plots indicated that although CO_2 production increased with temperature for both males and females, the magnitude of this increase varied by year (Fig. 2.3). Because the two-way interactions of temperature*year and sex*year were not significant, the significant three-way interaction indicated that one of the sexes had a different response to temperature in the two years. Comparisons of the mass-corrected variable by year for males and females at each temperature indicated that the differences were small. For females, sample sizes were small and variance was relatively larger. For males, the greatest difference in the means occurred at 20 and 25 °C. RMRs in males from 2000 tended to be slightly lower than 1999, leading to larger negative residuals that accounted for the three-way interaction (Table 2.3).

Thermal coefficients (Q_{10}) for both sexes were determined between 20 and 30 °C and also between 25 and 35 °C. RMR data for each sex were pooled at each of the four temperatures and yielded Q_{10} values of 2.0 (between 20 and 30 °C) and 2.3 (between 25 and 35 °C).

Respiratory Quotient (RQ)

$\dot{V}_{CO_2}$ measurements of 27 males and 14 females obtained from the constant-volume technique, were slightly higher than those measured from open-flow respirometry because I could not control for activity of the animals (Table 2.1). A mean RQ of 0.92 was calculated from data for all males and females combined.

Based on this RQ, I converted $\dot{V}_{CO_2}$ (ml CO_2 h^{-1}) to $\dot{V}_{O_2}$ (ml O_2 h^{-1}). These results together with mass-scaling equations expressed in μW at all four temperatures are presented in Table 2.4.

Evaporative Water Loss

Twenty-two males and six females were used to determine EWL and again females had a larger body mass (mean mass = 15.54 ± 0.81 g) compared to males (mean mass = 7.34 ± 0.29 g) ($t = 11.50$, $P < 0.01$). EWL at 30 °C was obtained for only two females so these data were removed from further analyses.

After log-transformation of the data, a graph of EWL versus body mass at each temperature indicated that females typically had lower rates of EWL than males (e.g., Fig. 2.4). Slopes of the log-transformed data were homogeneous between the sexes ($F_{1, 98} = 0.06$, $P = 0.81$), homogeneous across temperatures within each sex (females: $F_{2, 10} = 0.18$, $P = 0.83$; males: $F_{3, 74} = 0.08$, $P = 0.97$), and homogenous between sexes at each of the three temperatures (20 °C: $F_{1, 21} = 0.26$, $P = 0.61$; 25 °C: $F_{1, 22} = 1.36$, $P = 0.26$; 35 °C: $F_{1, 21} = 0.20$, $P = 0.67$). The scaling coefficients for these slopes and their corresponding intercepts are shown in Table 2.5.

Residuals (mass-corrected response variable) were calculated from the regression line determined from the relationship between $\log_{10}$ EWL and $\log_{10}$ body mass data for all individuals at all temperatures. The overall scaling relationship from this regression line was EWL = 0.69 * $\log_{10}$ M – 3.64 (where M is body mass in grams). The repeated-measures ANOVA for the mass-corrected EWL variable indicated that there was a significant two-way sex*temperature interaction ($F_{3,60} = 36.61$, $P < 0.001$). Examination of Figure 2.5 shows that EWL increased slowly between 20 and 30 °C and males had higher EWL than females at these temperatures. Once temperatures reached 35 °C, EWL increased substantially and females had higher EWL than males. This difference in response of males and females at low and high temperatures accounted for the two-way interaction. When EWL data at 35 °C are removed, the repeated-measures ANOVA indicated no significant sex*temperature interaction and EWL was influenced by temperature ($F_{2,37} = 28.49$, $P < 0.001$) and sex ($F_{1,28} = 7.74$, $P = 0.01$).

Thermal coefficients (Q_{10}) for EWL for both sexes were computed between 20 and 30 °C and between 25 and 35 °C. These were determined separately for males and females because of the substantial differences in EWL between the sexes at 35 °C. Mean Q_{10}s (between 20 and 30 °C) were 1.58 and 1.32 for females (n = 2 at 30 °C) and males, respectively. Between 25 and 35 °C, Q_{10}s were higher and, in addition, were more than twice as large in females compared to males (females $Q_{10} = 18.71$, males $Q_{10} = 8.66$)

Respiratory Water Economy

A repeated-measures ANOVA compared the index of effectiveness of water conservation (E) between the 22 males and five females for which there were both RMR and EWL data. Again for females, data at 30 °C were excluded from the analysis.

There was a significant sex*temperature interaction ($F_{1, 50} = 85.19$, $P < 0.01$) and examination of Fig. 2.6 indicates that for both males and females E decreased slightly from 20 to 30 °C and mean E of males and females was similar. Once temperatures reached 35 °C; however, there was an approximate 5-fold increase in E for males, but a more than 10-fold increase in E for females.

Discussion

Resting Metabolic Rates

As expected, RMRs for both males and females increased with body mass and temperature, with Q_{10}s in a normal physiological range. Metabolic rates in ml O_2 h^{-1} (Table 2.4) were similar to previously published data on tarantulas (females: three unidentified species from Mexico, Anderson 1970; Brachypelma smithi, Anderson and Prestwich 1985; males: Aphonopelma hentzi, Seymour and Vinegar 1973).

Sample sizes were smaller for females compared to males and this may explain some of the variability observed in the mass-scaling components for RMR (Table 2.1: ml CO_2 h^{-1}; Table 2.4: μW). Because results for males appeared more consistent, I compared only mass-scaling equations of RMR for males with other arthropods (Table 2.6). Metabolic rates measured in this study for male A. anax were approximately 30% of the predicted MRs for spiders (Lighton and Fielden 1995) at 25 °C. This is due both to a substantially reduced slope ($\log_{10}$ MR versus $\log_{10}$ body mass) and a lower intercept. At 30 and 35 °C, the allometric relationship between body mass and RMR for male tarantulas is more similar to that reported for many arthropods at 25 °C.

Among the arachnids, tarantulas are presumed to have comparatively low metabolic rates, and Anderson (1970) suggests that this is related to their relatively inefficient book-lung system. However, although this less efficient gas exchange and transport system may limit maximal aerobic metabolic rates, it seems an unlikely explanation for low RMRs. Low RMRs in tarantulas are more likely related to their low energy lifestyle (Bennett and Greenstone, 1980; Lighton and Fielden 1995; Lighton et al. 2001), which can include months of inactivity in a sealed burrow during the winter and during periods of molting, as well as periods of low food availability because of their sit-and-wait predatory strategy. Thus, they may have a low ratio of actively respiring tissue compared to overall body mass, leading to a low RMR (Lighton and Fielden 1995).

Sexual Dimorphism in RMR

The most interesting result of this study is that, after adjusting for body mass, RMRs at all temperatures were substantially higher for males than for females. Although Anderson (1970) decided against using male spiders in his experiments because of complications due to high activity patterns, the sensitivity of CO_2 analyzers and the resulting pattern of CO_2 production makes it very easy to determine when animals are active, and here such data were excluded.

Two out of four intraspecific comparisons of metabolic rates in spiders indicated that males had higher metabolic rates than females (Tanaka and Ito 1982; Watson and Lighton 1994). In a comparison of mass-specific MRs, Kotiaho (1998) found that males had lower metabolic rates than females, but analysis of mass-specific variables can result in false conclusions (Packard and Boardman 1988). Humphreys (1977) found no

differences between males and females, though metabolic rates did vary with season. Watson and Lighton (1994) measured metabolic rates of males within two days of mating and reported that rates were 63% higher than those of females. Although the prior mating encounter may have resulted in increased activity (Kotiaho 1998), Watson and Lighton (1994) indicated that they discarded recordings with active locomotion and/or grooming.

Both Kotiaho (1998) and Humphreys (1977) studied wolf spiders, a family of spiders that has many actively foraging species. As a result, adults of both sexes may have relatively similar life styles that involve regular locomotory activity. Although males are faced with higher energy costs associated with finding mates and courtship signaling (Kotiaho et al. 1998), the active predatory activities common to both males and females may have led to similar metabolic rates.

By comparison, life histories of mature males and females are substantially different among linyphiids (Watson and Lighton 1994) and tarantulas (this study), with males changing from a completely sedentary to a nomadic life style after reaching sexual maturity. As a result, I hypothesized that selection for increased mobility is likely associated with high field metabolic rates (Reinhold 1999), which in turn lead to increased RMR.

Rogowitz and Chappell (2000) found sexual differences in active metabolic rates of two species of eucalyptus-boring beetles. Males had a higher maximal rate of metabolism during activity, leading to greater maximal sustainable speeds compared to females. Because males search actively for receptive females, mating success is likely influenced by running ability and thus active metabolic rates. These males exhibit a similar mating strategy to male tarantulas. Comparison of RMR between the sexes was

inconclusive and a slight sexual dimorphism in RMR was reported for one species only.

Proximate causes for differences in RMRs between males and females may include differences in body composition, with females having a higher fat content (Brian et al. 1972, Cullum 1998). In spiders, mature females accumulate yolk in two steps (see Foelix 1996) and the first step is independent of mating. During the first step, while the egg grows and reaches a diameter of approximately 100 um, yolk particles also start to form (Foelix 1996). It is only after copulation that a second accumulation of yolk begins and this can take place only if enough food is available (Foelix 1996). As a result, even non-gravid females have larger proportions of protein and lipids in their abdomen than males and this may account for some of the differences in metabolic rates if the accumulated tissue has low metabolic activity (Carrel 1990).

Evaporative Water Loss

As with metabolic rates, after adjusting for mass, rates of EWL were higher in males than in females at lower temperatures (Fig. 2.5). In xeric-adapted arthropods, water loss at low temperatures occurs mostly by evaporation from the respiratory surfaces because the cuticle has a thick waxy layer that has limited water permeability (Davies and Edney 1952; Punzo and Jellies 1983; Pulz 1987). Thus, as metabolic rates increase with increasing temperature, air flow across the respiratory surfaces increases and, as a result, EWL increases (Anderson and Prestwich 1982). Because males have higher RMRs than females, it is not surprising that they also have higher rates of EWL. However, because male tarantulas experience increased exposure to more extreme habitats (Chapter 1), I hypothesized there would be strong selection in males for greater water conservation.

This hypothesis was supported by the comparisons of the effectiveness of water conservation (Fig. 2.6). At 35 °C, the substantial increase in E indicated a decreased water conservation that was more prevalent in females than males, i.e., at higher temperatures, females were less effective at conserving water.

In arachnids with book lungs (e.g., tarantulas), lung volume increases exponentially with body size (Anderson and Prestwich 1982). In addition, the largest lung volumes are found in those species with higher metabolic rates and the smallest in those with the lowest rates, i.e., respiratory surface area and metabolic rates (measured as O_2 consumption) increase in parallel (Anderson and Prestwich 1982). Although comparisons of surface area have been made between different species (Anderson and Prestwich 1982; Paul and Fincke 1989), no comparisons have been made between males and females of the same species. It is possible that female tarantulas, having lower metabolic rates, may also have a proportionally smaller lung surface area that may also account for the slightly lower rates of EWL compared to males at low temperatures (Fig. 2.5).

As temperatures rose above 30 °C, EWL increased substantially for both males and females. At higher temperatures, several spiders, including tarantulas, have been shown to secret or release fluids from the gnathocoxal gland (~ salivary glands) (Krakauer 1972; Pulz 1983, 1987; personal observation). This behavior, which is regularly accompanied by cheliceral and pedipal movement, results in reduced body temperatures and thus may be analogous to evaporative cooling in insects (Pulz 1987). Use of this evaporative cooling mechanism would account for increased EWL at 35 °C.

Rates of heating and cooling are faster in smaller animals because they have a larger ratio of surface area to volume than do larger animals. Under natural conditions, tarantulas can behaviorally avoid heat by retreating into burrows or shaded areas. However, this option is not available in a hot, enclosed space (respiratory chamber). Because larger animals lose heat more slowly across the body surface (low surface area to volume ratio), larger amounts of water may need to be secreted over time to avoid heat stress and this would account for the substantial difference in E between small males and large females at the hottest temperatures.

Conclusion

The results of this study show sexual dimorphism in whole-animal physiological traits (independent of body mass) in the tarantula A. anax. Because mating success in male tarantulas depends largely on their locomotory capabilities, adult males abandon their permanent retreats and spend considerable time and energy searching for receptive mates. As a result, males have a higher energy life style compared to females. This is reflected by their physiological capacities, which include such things as organ sizes and mitochondrial density. These factors in turn influence RMR. I hypothesize that selection for increased mobility is associated with the observed increased RMR.

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References

Anderson, J. F. (1970). Metabolic rates of spiders. *Comparative Biochemistry and Physiology* **33,** 51-72.

Anderson, J. F. (1994). Comparative energetics of comb-footed spiders (Araneae: Theriidae). *Comparative Biochemistry and Physiology* **109A,** 181-189.

Anderson, J. F. (1996). Metabolic rates of resting salticid and thomisid spiders. *Journal of Arachnology* **24,** 129-140.

Anderson, J. F. and Prestwich, K. N. (1982). Respiratory gas exchange in spiders. *Physiological Zoology* **55,** 72-90.

Anderson, J. F. and Prestwich, K. N. (1985). The physiology of exercise at and above maximal aerobic capacity in a theraphosid (tarantula) spider, *Brachypelma smithi* (F.O. Pickard-Cambridge). *Journal of Comparative Physiology B* **155,** 529-539.

Bartholomew, G.A. (1982). Energy metabolism. In *Animal Physiology* (ed. M.S. Gordon), pp. 46-93. New York: Macmillan.

Bartholomew, G.A. and Tucker, V.A. (1964). Size, body temperature, thermal conductance, oxygen consumption, and heart rate in Australian varanid lizards. *Physiological Zoology* **37**, 341-354.

Baerg, W. J. (1958). The Tarantula, pp. 88. Lawrence: University of Kansas Press.

Beaupre, S. J. (1993). An ecological study of oxygen consumption in the mottled rock rattlesnake, *Crotalus lepidus lepidus*, and the black-tailed rattlesnake, *Crotalus molossus molossus,* from two populations. *Physiological Zoology* **66,** 437-454.

Beaupre, S. J., Dunham, A. E. and Overall, K. L. (1993). Metabolism of a desert lizard: the effects of mass, sex, population of origin, temperature, time of day, and feeding on oxygen consumption of *Sceloporus merriami*. *Physiological Zoology* **66,** 128-147.

Beaupre, S. J. and Duvall, D. (1998). Variation in oxygen consuption of the western diamondback rattlesnake *(Crotalus atrox)*: implications for sexual dimorphism. *Comparative Physiology* **168B,** 497-506.

Bennett, A. F. and Dawson, W. R. (1976). Metabolism. In *Biology of Reptilia*, vol. 5 (ed. C. Gans), pp. 127-224. New York: Academic Press.

Brian, B.L., Gaffney, F.G., Fitzpatrick, L.C., and Scholes V.E.. (1972). Fatty acid distribution of lipids from carcass, liver and fat bodies of the lizard *Cnemidophorus tigris*, before hibernation. *Comparative Biochemistry and Physiology* **41B,** 661-664.

Carrel, J. E. (1990). Water and hemolymph content in the wolf spider *Lycosa ceratiola* (Araneae: Lycosidae). *Journal of Arachnology* **18,** 35-40.

Cloudsley-Thompson, J. L. 1991. Ecophysiology of desert arthropods and reptiles. Springer-Verlag, Berlin.

Cullum, A. J. (1998). Sexual dimorphism in physiological performance of whiptail lizards (Genus *Cnemidophorus*). *Physiological Zoology* **71,** 54-552.

Daan, S., Masman, D., and Groenewold, A. (1990). Avian metabolic rates: their

association with body composition in nature. *American Journal of Physiology* **259**, R333-R340.

Davies, M. E. and Edney, E. B. (1952). The evaporation of water from spiders. *Journal of Experimental Biology* **29**, 571-582.

Dunham, A.E., Grant, B.W., and Overall, K.L. (1989). Interfaces between biophysical and physiological ecology and the population ecology of terrestrial vertebrate ectotherms. *Physiological Zoology* **62**, 335-355.

Foelix, R. (1996). Biology of Spiders, pp. 330. Oxford: Oxford University Press.

Garland Jr., T. and Losos, J.B. (1994). Ecological morphology of locomotor performance in squamate reptiles. In *Ecological morphology: integrative organismal biology.* (eds. P. C. Wainwright and S. M. Reilly), pp 241-302. Chicago: University of Chicago Press.

Gessman, J.A. and Nagy, K.A. (1988). Energy metabolism: Errors in gass-exchange conversion factors. *Physiological Zoology* **61**, 507-513.

Greenstone, M. H. and Bennett, A. F. (1980). Foraging strategy and metabolic rate in spiders. *Ecology* **61,** 1255-1259.

Hebbalkar, D. S. and Sharma, R. N. (1991). Effects of age, sex, oogenetic cycles, body weight, juvenoids and precocene II on the oxygen consumption of the red cotton bug *Dysdercus koenigii* F. *Indian Journal of Experimental Biology* **29,** 962-966.

Humphreys, W. F. (1977). Respiration studies on *Geolycosa godeffroyi* (Araneae: Lycosidae) and their relationship to field estimates of metabolic heat loss. *Comparative Biochemistry and Physiology* **57A,** 555-563.

Jameson, E. W., Heusner, A. A. and Arbogast, R. (1976). Oxygen consumption of *Sceloporus occidentalis* from three different elevations. *Comparative Biochemistry and Physiology* **56A,** 73-79.

Kaiser, T. J. and Bucher, T. L. (1985). The consequences of reverse sexual size dimorphism for oxygen consumption, ventilation and water loss in relation to ambient temperature in the Prairie Falcon *Falco mexicanus*. *Physiological Zoology* **58,** 748-758.

Koteja, P. (1991). On the relation between basal and field metabolic rates in birds and mammals. *Functional Ecology* **5,** 56-64.

Kotiaho, J. S. (1998). Sexual differences in metabolic rates of spiders. *Journal of Arachnology* **26,** 401-404.

Kotiaho, J. S., Alatalo, R. V., Mappes, J., Nielsen, M. G., Parri, S. and Rivero, A. (1998). Energetic costs of size and sexual signalling in a wolf spider. *Proceedings of the Royal Society of London* **265,** 2203-2209.

Krakauer, T. (1972). Thermal response of the orb-weaving spider *Nephilia clavipes* (Araneae: Argiopidae). *American Midland Naturalist* **88,** 245-250.

Lighton, J. R. B. and Fielden, L. J. (1995). Mass scaling of standard metabolism in ticks: A valid case of low metabolic rates in sit-and-wait strategists. *Physiological Zoology* **68,** 43-62.

Lighton, J.R.B., Brownell, P.H., Joos, B. and Turner, R.J. (2001). Low metabolic rate in scorpions: implications for population biomass and cannibalism. Journal of Experimental Biology **204**, 607-613.

Maloney, S. K. and Dawson, T. J. (1993). Sexual dimorphism in basal metabolism and body temperature of a large bird, the emu. *Condor* **95,** 1034-1037.

Nagy, K.A. and Peterson, C.C. (1988). Scaling of water flux rate in animals, pp. 172, Berkeley: University of California Publications

Packard, G. C. and Boardman, T. J. (1988). The misuse of ratios, indices, and percentages in ecophysiological research. *Physiological Zoology* **61,** 1-9.

Paul, R. and Fincke, T. (1989). Book lung function in arachnids II. Carbon dioxide release and its relations to respiratory surface, water loss and heart frequency. *Journal of Comparative Physiology B* **159,** 419-432.

Penteado, C. H. S. and Hebling-Beraldo, M. J. A. (1991). Oxygen consumption related to size and sex in the tropical millipede *Psedonannolene tricolor* (Diplopoda: Spirostreptida). *Comparative Biochemistry and Physiology* **98A,** 265-269.

Peterson, C.C. (1990). Paradoxically low metabolic rate of the diurnal gecko *Rhoptropus afer*. *Copeia* **1990**, 233-237.

Pulz, R. (1983). Patterns of evaporative water loss in tarantulas (Araneae: Theraphosidae): transpiration and secretion. In *Proceedings of the Ninth International Congress of Arachnology* (ed. W. G. Eberhard, Y. D. Lubin and B. C. Robinson), pp. 197-201. Panama: Smithsonian Institute Press.

Pulz, R. (1987). Thermal and water relations. In *Ecophysiology of Spiders* (ed. W. Nentwig), pp. 26-55. Berlin: Springer-Verlag.

Punzo, F. and Jellies, J. (1983). Comparative water relations of araneid and lycosid spiderlings. *Comparative Biochemistry and Physiology* **74A,** 981-988.

Reinhold, K. (1999). Energetically costly behaviour and the evolution of resting metabolic rate in insects. *Functional Ecology* **13,** 271-224.

Ricklefs, R. E. and Miles, D. B. (1994). Ecological and evolutionary inferences from morphology: an ecological perspective. In *Ecological Morphology: Integrative Organismal Biology* (ed. P. C. Wainwright and S. M. Reilly), pp. 13-41. Chicago: University of Chicago Press.

Rintamaki, H., Karplund, L., Linden, H. and Hissa, R. (1984). Sexual differences in temperature regulation and energetics in the capercaillie, *Tetrao urogallus*. *Ornis Fenn* **61,** 69-74.

Rogowitz, G. L. and Chappell, M. A. (2000). Energy metabolism of eucalyptus-boring beetles at rest and during locomotion: gender makes a difference. *Journal of Experimental Biology* **203,** 1131-1191.

Sanborn, C. F. and Jankowski, C. M. (1994). Physiologic considerations for women in sport. *Clinical Sports Medicine* **13,** 315-327.

Seymour, R. S. and Vinegar, A. (1973). Thermal relations, water loss and oxygen consumption of a North American tarantula. *Comparative Biochemistry and Physiology* **44A,** 83-96.

Shillington, C. and Verrell, P. (1997). Sexual strategies of a North American 'tarantula' (Araneae: Theraphosidae). *Ethology* **103,** 588-598.

Tanaka, K. and Ito, Y. (1982). Decrease in respiratory rate in a wolf spider, *Pardosa astrigera*(L. Koch), under starvation. *Researches in Population Ecology* **24,** 360-374.

Watson, P. J. and Lighton, J. R. B. (1994). Sexual selection and the energetics of copulatory courtship in the Sierra dome spider, *Linyphia litigiosa*. *Animal Behaviour* **48,** 615-626.

Withers, P.C. (1977). Measurements of $\dot{V}_{O_2}$, $\dot{V}_{CO_2}$ and evaporative water loss with a flow-through mask. *Journal of Applied Physiology* **42**, 120-123.

Table 2.1: The allometric relationship between RMR and body mass for male and female tarantulas at 20, 25, 30 and 35 °C. This is based on results of least-squared regression of $\log_{10} \dot{V}_{CO_2}$ (ml h^{-1}) on $\log_{10}$ body mass (g). Metabolic rates measured at 25 °C using the constant-volume technique* are included for comparison with flow-through RMR values.

	N	Body Mass† (g)	MR (ml CO_2 h^{-1}) † (constant volume)*	RMR† (ml CO_2 h^{-1})	Intercept¶ Log (ml h^{-1})	Slope¶	Equation for RMR (ml CO_2 h^{-1})
Females:							
20 °C	12	12.73 ± 1.32		0.11 ± 0.01	-1.49 ± 0.49	0.45 ± 0.44	0.033 $M^{0.446}$
25 °C	10	13.19 ± 1.39	0.31 ± 0.03	0.16 ± 0.02	-2.21 ± 0.25	1.25 ± 0.23	0.006 $M^{1.249}$
30 °C	13	13.88 ± 1.53	(n=14)	0.33 ± 0.09	-1.31 ± 0.49	0.65 ± 0.43	0.049 $M^{0.652}$
35 °C	12	13.92 ± 1.41		0.37 ± 0.03	-1.05 ± 0.27	0.53 ± 0.23	0.089 $M^{0.534}$
Males:							
20 °C	43	7.62 ± 0.34		0.13 ± 0.01	-1.47 ± 0.14	0.62 ± 0.16	0.062 $M^{0.617}$
25 °C	38	7.78 ± 0.36	0.33 ± 0.02	0.21 ± 0.01	-1.26 ± 0.13	0.64 ± 0.14	0.056 $M^{0.644}$
30 °C	40	7.63 ± 0.34	(n=27)	0.28 ± 0.01	-1.30 ± 0.09	0.86 ± 0.11	0.050 $M^{0.860}$
35 °C	37	7.48 ± 0.37		0.42 ± 0.03	-1.23 ± 0.11	0.86 ± 0.13	0.075 $M^{0.860}$

† values are means ± S.E.M.

¶ values include standard error of the slope and intercept

Table 2.2: Repeated-measures analysis for the effects of sex and temperature and year and their interactions on log-transformed RMRs (ml CO_2 h^{-1}) of male and female tarantulas.

Source	df	F Value	P
Between Subjects			
sex	1,68	46.73	< 0.01
year	1, 67	0.49	0.49
sex*year	1, 68	1.34	0.42
Within Subjects			
temperature	3, 148	99.23	< 0.01
temperature * sex	3, 148	0.60	0.61
temperature * year	3,148	1.21	0.31
temperature * sex * year	3, 148	4.47	0.05

Table 2.3: Comparison of mass-residuals of RMR (log_{10} ml CO_2 h^{-1}) by year for male and female tarantulas at each temperature.

	20 °C	25 °C	30 °C	35 °C
Females:				
mean difference between years	-0.19	-0.11	+0.13	+0.06
t value	-1.69	-1.02	0.85	1.08
P	0.12	0.34	0.41	0.31
Males:				
mean difference between years	+0.09	+0.13	-0.006	-0.06
t value	2.01	3.24	-0.25	-0.20
P	0.05	0.002	0.81	0.52

Table 2.4: Mean RMRs reported in ml O_2 h^{-1} for male and female tarantulas. RMRs were converted from ml CO_2 h^{-1} (Table 1) using an RQ = 0.92. The mass scaling equations for RMR in microwatts are also presented for each temperature. M in the scaling equations is body mass measured in grams. See Table 2.1 for body masses.

	RMR (ml O_2 h^{-1})	Equation for RMR (μW)
Females:		
20 °C	0.12	204.17 $M^{0.456}$
25 °C	0.17	39.36 $M^{1.249}$
30 °C	0.35	311.1 $M^{0.652}$
35 °C	0.40	564.70 $M^{0.534}$
Males:		
20 °C	0.15	225.28 $M^{0.617}$
25 °C	0.23	394.94 $M^{0.644}$
30 °C	0.30	313.74 $M^{0.860}$
35 °C	0.46	471.30 $M^{0.860}$

Table 2.5: The allometric relationship between EWL and body mass for male and female tarantulas at 20, 25, 30 and 35 °C. This is based on results of least-squared regression of $\log_{10}$ EWL (g h^{-1}) on $\log_{10}$ body mass (g). M in the equation for EWL is body mass measured in grams.

	N	Body mass † (g)	EWL† (g h^{-1})	Intercept¶ (g h^{-1})	Slope¶	Equation for EWL (g h^{-1})
Females:						
20 °C	5	15.41 ± 2.04	$4.4 \times 10^{-4} \pm 7.2 \times 10^{-5}$	-4.64 ± 0.37	1.10 ± 0.32	$2.3 \times 10^{-5}\ M^{1.10}$
25 °C	6	16.99 ± 1.11	$7.6 \times 10^{-4} \pm 9.1 \times 10^{-5}$	-4.15 ± 0.38	0.85 ± 0.32	$7.1 \times 10^{-5}\ M^{0.854}$
35 °C	5	13.31 ± 1.58	$126.3 \times 10^{-4} \pm .0015$	-3.04 ± 0.23	0.97 ± 0.20	$91.4 \times 10^{-5}\ M^{0.966}$
Males:						
20 °C	20	7.44 ± 0.61	$4.4 \times 10^{-4} \pm 3.7 \times 10^{-5}$	-4.03 ± 0.14	0.76 ± 0.12	$93.3 \times 10^{-5}\ M^{0.762}$
25 °C	22	7.42 ± 0.61	$5.8 \times 10^{-4} \pm 5.6 \times 10^{-5}$	-3.94 ± 0.15	0.79 ± 0.14	$11.5 \times 10^{-5}\ M^{0.794}$
30 °C	19	7.36 ± 0.54	$5.6 \times 10^{-4} \pm \times 10^{-5}$	-3.88 ± 0.08	0.72 ± 0.11	$13.1 \times 10^{-5}\ M^{0.725}$
35 °C	21	7.22 ± 0.49	$49.3 \times 10^{-4} \pm 3.8 \times 10^{-4}$	-2.93 ± 0.10	0.71 ± 0.12	$118.8 \times 10^{-5}\ M^{0.711}$

† values are means ± S.E.M.

¶ values include standard error of the slope and intercept

Table 2.6: Comparison of mass-scaling equations (corrected to 25 °C) for RMR for several different arthropod taxa. M in the equations for RMR is body mass measured in grams.

Equation for RMR (μW)	Source of Equation
906 $M^{0.825}$	Lighton and Fielden 1995 (spiders)
888 $M^{0.816}$	Lighton and Fielden 1995 (ants, beetles, spiders)
110 $M^{0.816}$	Lighton and Fielden 1995 (ticks)
236 $M^{0.856}$	Lighton et al. 2001 (scorpions)
708 $M^{0.816}$	Vogt and Appel (1999) (fire ant Solenopsis invicta)
394.94 $M^{0.643}$	this study (A. anax males)

List of Figures

Figure 2.6: Comparison of the index of effectiveness of water conservation (E) between males and female tarantulas at 20, 25, 30 and 35 °C. E is the ratio of EWL (ml h^{-1}) to RMR (ml CO2 h^{-1}) between individual animals.

FIGURE 2.1: RMR versus body mass.

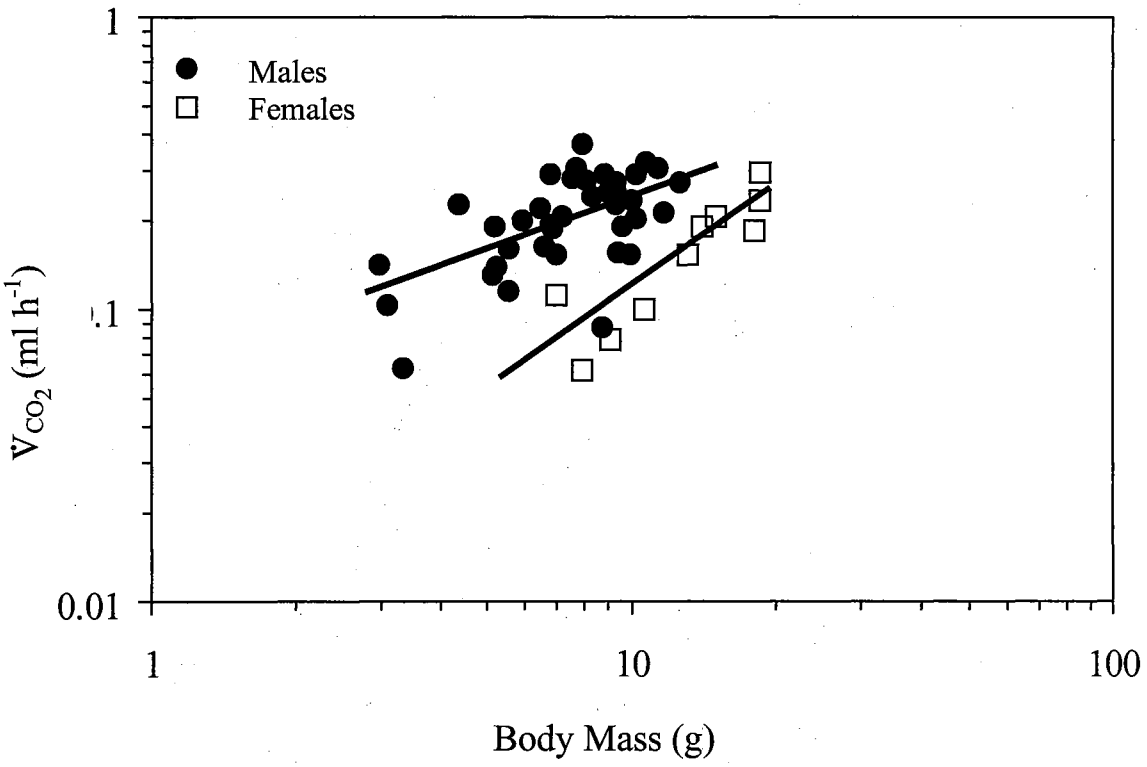


FIGURE 2.2: Mass-corrected RMR versus temperature.

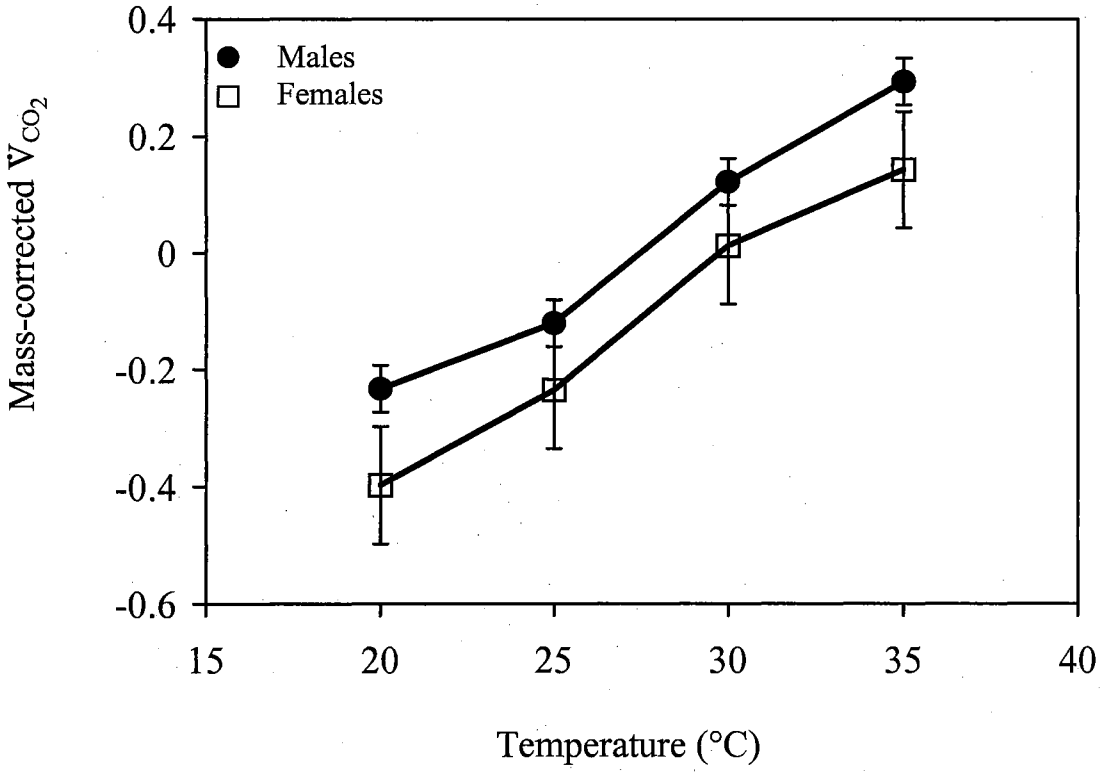


FIGURE 2.3: Comparison of RMR by year.

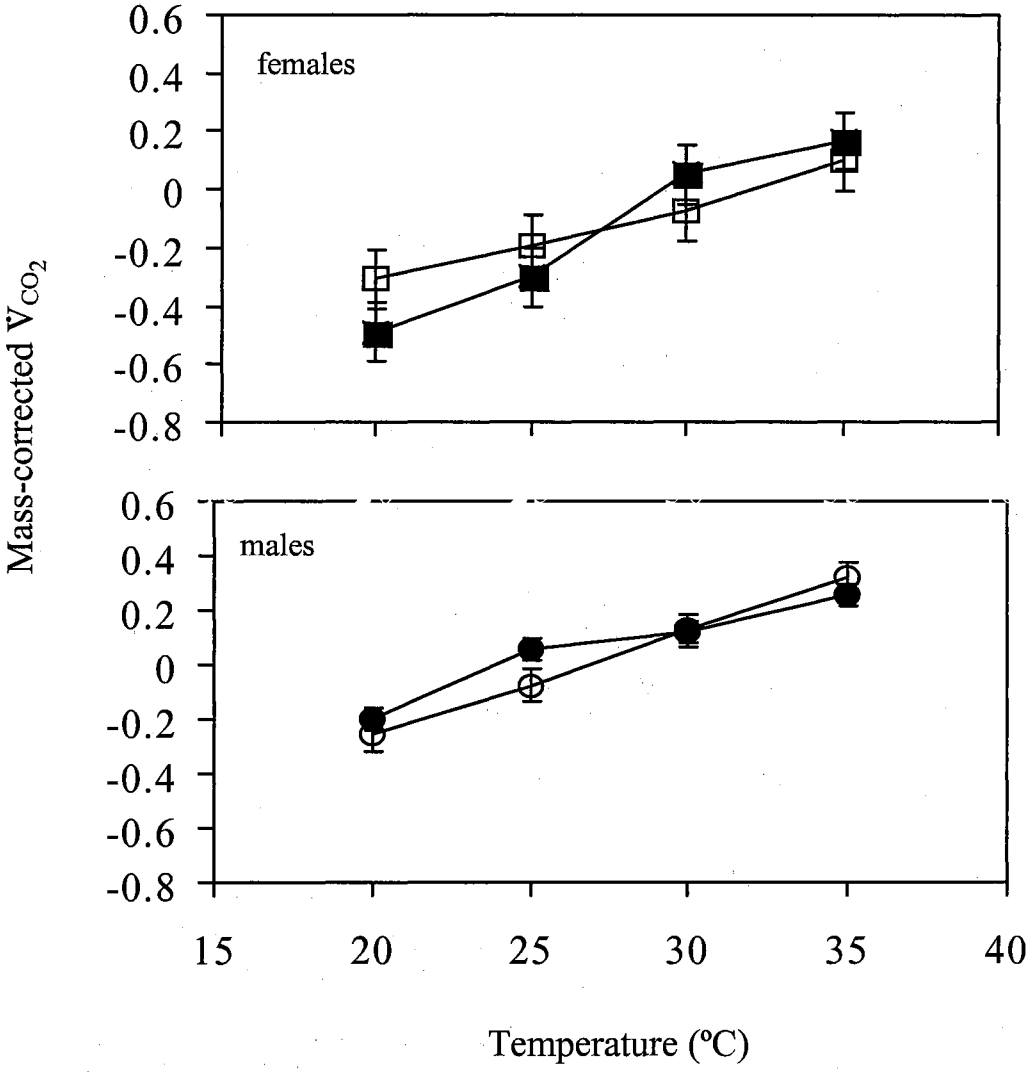


FIGURE 2.4: EWL versus body mass.

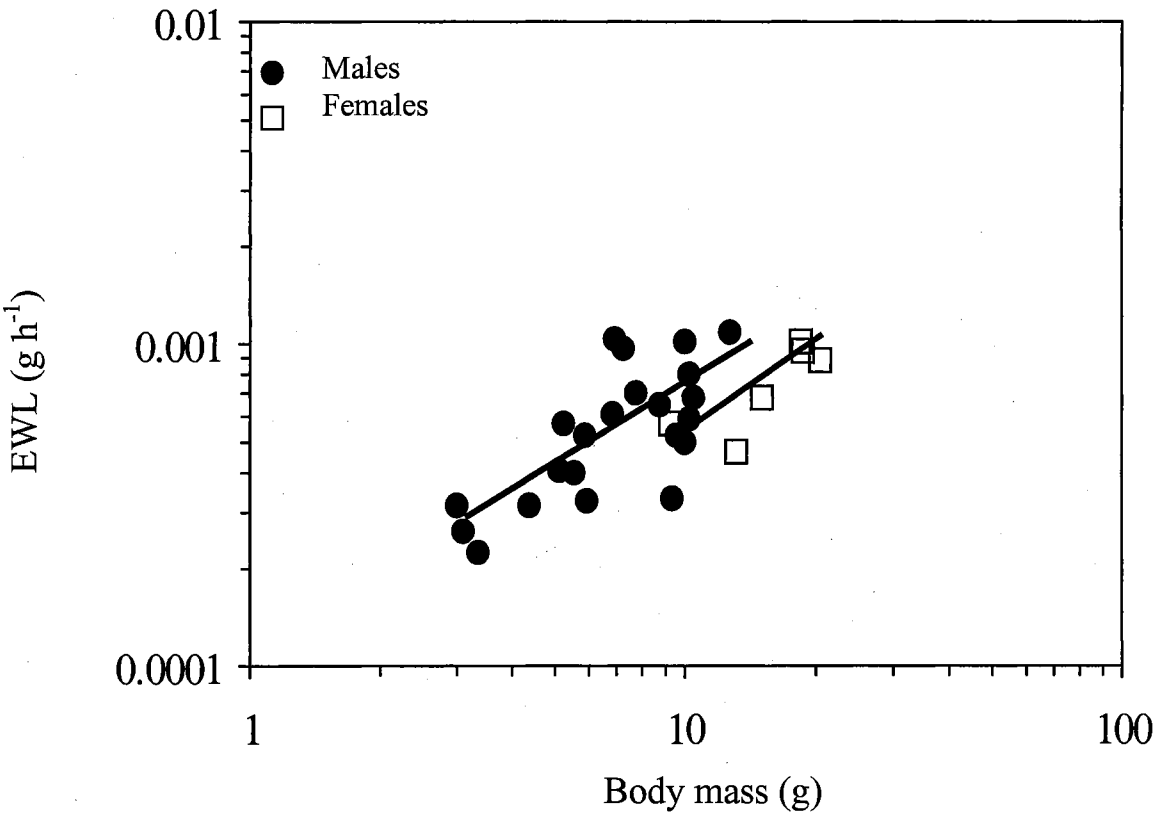


FIGURE 2.5: Mass-corrected EWL versus temperature.

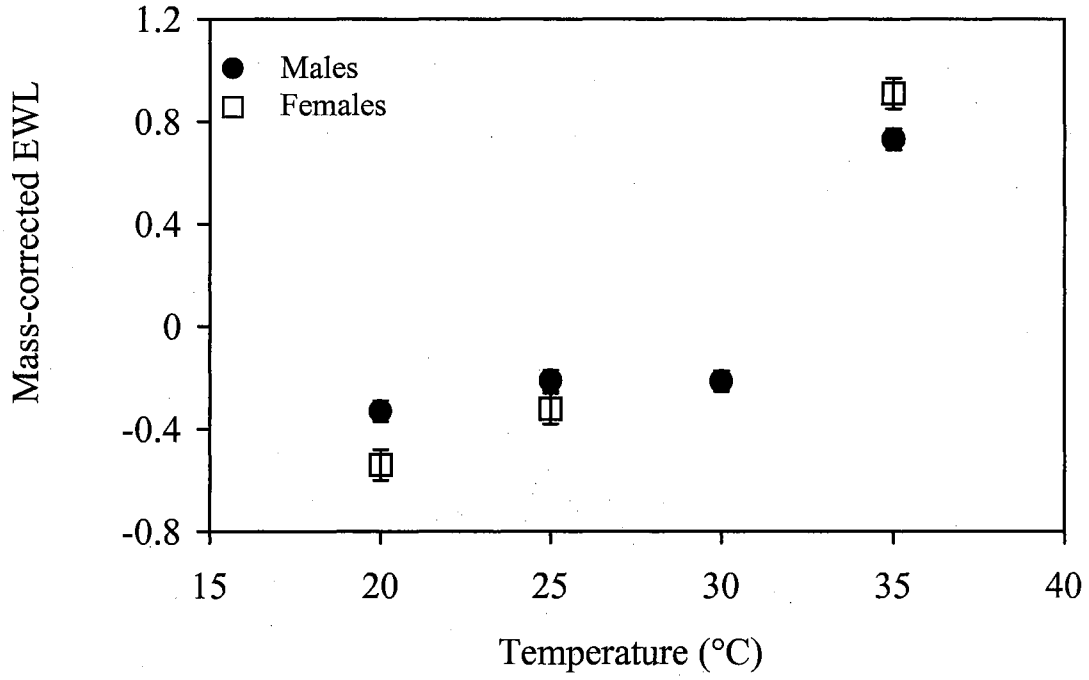
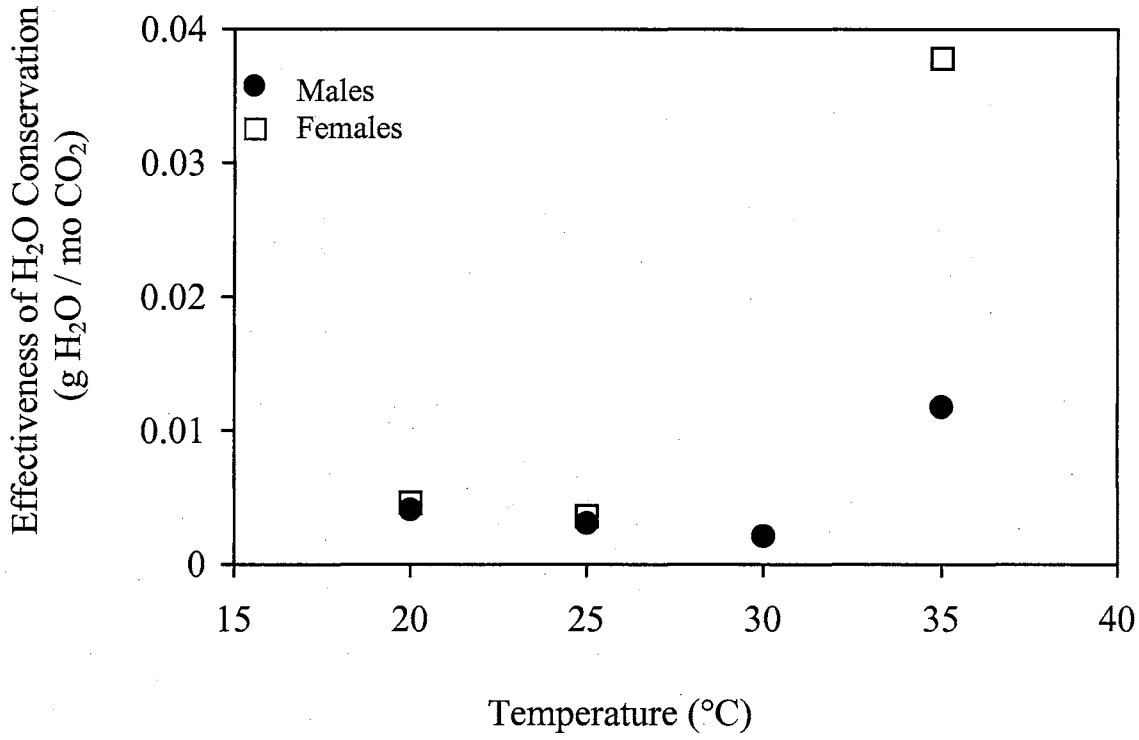


FIGURE 2.6: Effectiveness of water conservation at each temperature.



CHAPTER 3

ENERGY METABOLISM OF MALE AND FEMALE TARANTULAS (*APHONOPELMA ANAX*) DURING LOCOMOTION

Summary

I 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 that are fossorial and sedentary. Because of this dimorphism in life history, I predicted that selection in males would enhance their abilities to sustain high levels of aerobic metabolism (compared to 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 rate of carbon dioxide production ($\dot{V}_{CO_2}$) increased within the range of sustainable aerobic speeds for both males and females. Although there was substantial variation in physiological performance traits among individuals, there was no detectable sexual dimorphism in maximal aerobic capacity ($\dot{V}_{CO_2max}$), maximal aerobic speed (MAS), or minimum cost of transport (C_{min}).

Introduction

Numerous studies of the energetics of terrestrial locomotion have focused on aerobic energy expenditure during activity, and the impact of different activities and different intensities of activity on energy budgets of animals (e.g., Taylor et al., 1970;

Herreid, 1981; Taylor and Heglund, 1982; Taylor et al., 1982; Gatten et al., 1992). Variation in energy expenditure is strongly influenced by environmental factors (e.g., temperature and time of day) and intrinsic factors such as body mass or sex (Bennett and Dawson,1976; Beaupre, 1993; Beaupre et al., 1993), and may in turn influence net allocation of energy to growth, storage, and reproduction. Thus, differences in patterns of energy allocation within and among individuals may have important effects on behavior and life history (Greenstone and Bennett, 1980; Beaupre and Duvall, 1998; Autumn et al., 1999).

Within species, sexual dimorphism in morphology and behavior has been extensively studied; however, dimorphism in physiological performance (e.g., speed, endurance and 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). Sexual dimorphism in size and life history is prevalent among spiders (Foelix, 1996), leading to differences in energetic requirements. After reaching sexual maturity, male spiders change their habits and leave their retreats or webs and search actively for females. Males are relatively short-lived and the energy used in gamete production is small (though cost of locomotion may be high). Females maintain a larger body size over a longer life span and also have a higher energetic cost associated with gamete production and, in some species, parental care (Foelix, 1996). Energetic requirements associated with these different lifestyles and mating strategies may in turn have led to the evolution of differential metabolic rates and capacities between males and females (Snell et al.,

1988; Garland, 1993; Reinhold, 1999; Rogowitz and Chappell, 2000). A similar co-adaptation between maximal aerobic rates and physiological performance traits has been suggested for several reptiles and amphibians (Taigen et al., 1982; Pough et al., 1992; Garland, 1993; Walton et al., 1994). However, these comparisons are typically between different species.

The goal of this study was to compare metabolic rates of male and female tarantulas (Aphonopelma anax) during locomotion to determine if the sexes differed in physiological performance traits such as maximum aerobic speed (MAS), maximal rate of CO_2 production ($\dot{V}_{CO_2max}$) and minimum cost of transport (C_{min}). This species displays dimorphism in life history that is typical of most fossorial tarantulas. Females are sit-and-wait predators that usually remain within close proximity of their burrows for their entire lives. Alternatively, once males reach sexual maturity, they abandon their burrows and search actively for well-dispersed mates. 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, I predicted that males would have a higher $\dot{V}_{CO_2max}$, reflecting a greater capacity for aerobic power output, and thus higher sustainable locomotory speeds compared to females, as well as greater locomotory efficiency (i.e., lower C_{min}).

Methods and Materials

Study Animals

Male and female tarantulas (Aphonopelma anax) 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. Animals were transported to Oklahoma State University and maintained in the laboratory in individual 3.8-liter containers under a natural photoperiod (14:10 light:dark), and at a room temperature 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

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

Tarantulas were placed into the smaller chamber and left undisturbed for 30 minutes. Prior to exercise I measured resting metabolic rates (RMRs). After this rest period, the treadmill was activated at a slow speed (~ 25 m h^{-1}). When the treadmill was initially activated, many animals displayed erratic movements, but these behaviors

usually ceased after a few minutes as animals became accustomed to the movement. With animals that continued to show erratic movement patterns and bursts of speed after five minutes, I increased treadmill speed until even-paced movement was achieved. $\dot{V}_{CO_2}$ measurements were recorded only at speeds that were sustainable for at least 20 minutes, in an attempt to minimize anaerobic respiration. Steady-state $\dot{V}_{CO_2}$ (cost of locomotion) for an individual was recorded during the last five minutes of continuous locomotion at each speed. Over time, speeds were increased until speeds were reached where the animals could not maintain even-paced locomotion for a 20-minute period. If animals stumbled at higher speeds, I 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 123.3 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 between 24 – 26 °C.

$\dot{V}_{CO_2}$ was calculated from fractional concentrations of CO_2 entering (Fi) and leaving (Fe) the respirometry chamber using the equation from Withers (1977):

$$\dot{V}_{CO_2} \text{ (ml h}^{-1}) = (Fe_{CO_2} - Fi_{CO_2}) * \text{(flow rate in ml h}^{-1})$$

Fi was zero because incoming air initially passed through the scrubbing column. In addition, to compare my results with previous studies in which metabolic rates are usually reported as rates of oxygen consumption ($\dot{V}_{O_2}$) , I converted my raw data from $\dot{V}_{CO_2}$ to $\dot{V}_{O_2}$ using a respiratory quotient (RQ) of 0.92 for both males and females (Chapter 2).

Maximum Aerobic Speed, $\dot{V}_{CO_2\,max}$ and Minimum Costs of Locomotion (C_{min})

By analogy with oxygen consumption, $\dot{V}_{CO_2}$ typically increases with speed in a linear manner until $\dot{V}_{CO_2\,max}$ is reached (Bennett, 1982; Gatten et al., 1992). $\dot{V}_{CO_2\,max}$ 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; Schmidt-Nielsen, 1996). I defined $\dot{V}_{CO_2\,max}$ for each individual as the $\dot{V}_{CO_2}$ achieved when an increase in speed resulted in no significant increase in $\dot{V}_{CO_2}$. This was determined from examination of plots of $\log_{10} \dot{V}_{CO_2}$ versus $\log_{10}$ speed for each individual. MRs in the anaerobic range were not related to speed ($\underline{r} = 0.45$, $\underline{P} = 0.19$) and were excluded from analyses.

Results

Comparison between Individuals

Prior to activating the treadmill, I attempted to measure RMRs. However, several animals continuously explored the chamber during this time so I used RMRs determined previously for these individuals (Chapter 2). Previously measured RMRs were similar to RMRs of animals that remained quiescent on the treadmill ($n = 5$, paired-$t = -0.78$, $\underline{P} = 0.50$).

The locomotory behavior of tarantulas on the treadmill resembled natural locomotion (personal observation). Typically, movement was initiated when the trailing

legs came in 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 CO_2 h^{-1}) increased with increasing speed for both males and females (repeated-measures ANCOVA: $F_{4,21} = 19.07$, $P < 0.01$).

For each individual, I plotted the relationship between $\dot{V}_{CO_2}$ (ml h^{-1}) and speed (m h^{-1}). From regression analyses of this relationship, I obtained a y-intercept and slope (C_{min}). These values are presented in Table 3.1 together with $\dot{V}_{CO_2max}$ and MAS. One male and three females achieved anaerobic speeds (indicated in Table 3.1, Figs. 3.1 and 3.2). For the remaining animals, $\dot{V}_{CO_2}$ increased linearly to the fastest speed achieved, so $\dot{V}_{CO_2max}$ and MAS are probably underestimated for these individuals. The absolute maximum speed reached by an 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 well within her anaerobic range (MAS = 36.4 m h^{-1}), she sustained this level of activity for approximately 20 minutes. More typically, beyond MAS animals were not able to maintain even-paced locomotion on the treadmill and they either stumbled continuously or climbed partially onto the walls of the animal chamber to escape the moving treadmill.

C_{min} differed among individuals in each sex (test for homogeneity of slopes: females: $\underline{F}_{5,12} = 22.04$, $\underline{P} < 0.01$; males: $\underline{F}_{5,12} = 13.48$, $\underline{P} < 0.01$) and the y-intercepts were approximately 2 – 3 times higher than RMRs (Table 3.1). For one female, it was not possible to determine a slope because she appeared to be using anaerobic respiration at all but the lowest speed. For comparison with literature values, I converted raw $\dot{V}_{CO_2}$

(ml hr^{-1}) data to $\dot{V}_{O_2}$ (ml h^{-1}) using an RQ of 0.92. For each individual, I plotted the relationship between metabolic rate versus speed (km h^{-1}), this time using mass-specific $\dot{V}_{O_2}$ (ml g^{-1} h^{-1}) and determined C_{min} (expressed as ml g^{-1} km^{-1}) from the regression analyses (Table 3.2). Mass-specific C_{min} showed a weak tendency to decrease with increasing mass ($\underline{r}$ = -0.35, $\underline{P}$ = 0.28) (Fig. 3.3).

Factorial scopes (which indicate an individual's ability to increase MR above RMR) were calculated as $\dot{V}_{CO_2max}$/RMR. Factorial scopes were highly variable among individuals (Table 3.1). $\dot{V}_{CO_2max}$ averaged 12.75 times greater than RMR for females and 10.80 times greater than RMR for males (t-test: t = 0.51, P = 0.62).

Intersexual Comparisons

I compared $\dot{V}_{CO_2max}$ (ml h^{-1}) and C_{min} (ml CO_2 m^{-1}), and MAS (m h^{-1}) between males and females. Prior to analyses, I log-transformed these variables and tested for the effect of body mass (also log-transformed). Body mass was not a covariate of V_{CO_2max}, C_{min} or MAS and analyses of these variables indicated that there was no sexual dimorphism in $\dot{V}_{CO_2max}$ (ANOVA: $\underline{F}_{1,8}$ = 1.61, $\underline{P}$ = 0.24), MAS (ANOVA $\underline{F}_{1,8}$ = 0.59, $\underline{P}$ = 0.47), or C_{min} (ANOVA: $\underline{F}_{1,7}$ = 0.16, $\underline{P}$ = 0.70).

$\dot{V}_{CO_2}$ (ml h^{-1}) was 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 $\dot{V}_{CO_2}$ and mass-scaling slopes ($\log_{10} \dot{V}_{CO_2}$ versus $\log_{10}$ body mass) were homogeneous for males and females at each of the three speeds, I used an ANCOVA. $\dot{V}_{CO_2}$ was similar between males and females at each speed (Table 3.3).

Discussion

The main purpose of this study was to determine if differences in life history between adult 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 within increasing speed in both male and female A. anax (Figs. 3.1 and 3.2). A similar linear increase in V_{O_2} and $\dot{V}_{CO_2}$ is reported in other invertebrates (e.g., cockroaches: Herreid, 1981; Herreid and Full, 1984; crabs: Full 1987; beetles: Lighton, 1985; Rogowitz and Chappell, 2000) and vertebrates (Taylor et al., 1970; Bennett, 1982; Taylor et al., 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 chamber as speeds advanced beyond a slow walk. However, this does not necessarily indicate an inability to move at higher speeds; one 14-g female attained the high speed of 126.3 mh^{-1}. In addition, large females with big abdomens tended to hold their bodies closer to the

ground whereas smaller and lighter females and males had a more elevated posture during locomotion. Only three of the six females reached speeds where they became anaerobic; thus, empirical $\dot{V}_{CO_2max}$ 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-minute rest period prior to exercise. These differences are consistent with observations of males and females maintained in the laboratory (personal observation). Although males had smaller abdomens and longer legs (Chapter 2), MAS of males was very similar to that of females. Only one of six males reached anaerobic speeds (Fig. 3.2), suggesting empirical MAS and $\dot{V}_{CO_2max}$ underestimated performance ability. On the other hand, males were more likely to stumble and lose balance at higher speeds compared to females who simply refused to move. One possible explanation for this is the age and physical condition of the males. All males used in this study died within 6 to 8 weeks after 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 age and physical condition. This idea is further supported by the fact that one male, freshly collected in Oklahoma (different 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 minutes without stumbling, which is 2-3 times the speeds achieved by any of the males in this study. However, these high speeds were anaerobic; MAS and MMR for this male were similar to those found with A. anax males. In addition, the Oklahoma male survived more than six months beyond the completion of this study.

Maximum rates of aerobic respiration and factorial scope

Maximum rates of aerobic respiration and factorial scopes have been reported for females of two other tarantula species (Theraphosinae: species unknown; Herreid, 1981 and Brachypelma smithi; Anderson and Prestwich, 1985). $\dot{V}_{CO_2max}$ is relatively similar between these species; however, A. anax females had higher factorial scopes and lower MAS than the two other species at similar temperatures (Table 3.4). The 2-fold differences in factorial scope between A. anax and the unknown species (Herreid, 1981) is due to the substantially lower RMR measured for A. anax, nearly three times lower than those reported by Herreid (1981). Differences in RMR may be due to different laboratory techniques, restlessness of animals in metabolic chambers, or different life styles, habitats, or growth rates between the two species (Chappell, 1983; Anderson, 1994).

Although there has been one study of metabolic rates during activity in male tarantulas (Seymour and Vinegar, 1973), few raw data or means are reported. Tarantulas fatigued within 2-7 minutes (depending on temperature) in that study, which suggests that they were beyond maximal aerobic activity. Thus, the reported factorial scopes (3.6 at 20 °C and 6.4 at 30 °C) in the Seymour and Vinegar (1973) study may not be reliable.

Previous studies indicate that factorial scopes of spiders range from 2 to 10 (Miyashita, 1969; Seymour and Vinegar, 1973; Peakall and Witt, 1976; Ford, 1977; Humphreys, 1977; Prestwich, 1977; McQueen, 1980; Anderson and Prestwich, 1982). Anderson and Prestwich (1982) suggest that this range may be limited in part by physiological factors such as circulation, heart rate, ventilation and respiratory surface area. Factorial scopes for individual A. anax in my study were quite variable and were often higher than those reported for other tarantulas (Seymour and Vinegar, 1973; Herreid, 1981), but they were usually within the range (5- to 15-fold) reported for mammals (Taylor et al., 1970), reptiles (Bennett, 1982), and some crustaceans (Full and Herreid, 1983).

Minimum cost of transport (C_{min})

Based on several interspecific comparsions among diverse taxa, locomotion in small animals is less energetically economical than in large animals on a mass-specific basis (mammals and birds: Taylor et al., 1982; reptiles: Bennett, 1982; insects: Herreid, 1981, Lighton, 1985; crustaceans: Full, 1987). However, Walton et al. (1994) found that mass-specific C_{min} was independent of body mass for northern toads (Bufo boreaus halophilus). I found a similar lack of relationship with A. anax (Fig. 3.3).

C_{min} is widely used in interspecific comparisons but is typically reported in units of mass-specific oxygen consumption (ml O2 g^{-1} h^{-1}). When converted to these units, mean C_{min} for both male and female tarantulas was very similar to the predicted values calculated using the C_{min}-mass scaling equation determined for several insect taxa (Lighton 1985) (based on male and female tarantulas with body masses of 15.72 g and

6.91 g respectively) (Table 3.5). An analogous comparison can be made using the C_{min}-mass scaling equation provided by Gatten et al. (1992), which includes data from more diverse taxa (e.g., birds, mammals, reptiles, crustaceans and insects). The predicted C_{min} is again similar to my results (Table 3.5). Predicted values of C_{min} are included for comparison in Figure 3. However, a previous study reported a C_{min} for tarantulas that is approximately a factor of 10 lower than C_{min} for A. anax (Herreid, 1981). Tarantulas in this previous study were run at substantially higher velocities (100 – 250 m h^{-1}) than my study, and Herreid (1981) suggests that there may have been a large anaerobic contribution leading to the exceptionally low C_{min}.

Sexual dimorphism in metabolic rates and performance traits

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

After adjusting for the effects of body mass (ANCOVA with mass as a covariate), there were no differences between the sexes in whole-animal submaximal $\dot{V}_{CO_2}$ during activity. In addition, factorial scopes, $\dot{V}_{CO_2max}$, C_{min}, and MAS (which were independent of body mass) were similar for both groups (Table 3.1). 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, good

circulatory system and 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 compared to hemoglobin (Paul et al., 1992). Thus, males may be physiologically incapable of higher $\dot{V}_{CO_2max}$ despite having higher RMR compared to females (Chapter 2). Additional research is needed to address questions related to physiological limitations and also to examine the potential influence of age and physical conditions on 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 (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). 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 also needed to examine the role of anaerobic metabolism in active male and female tarantulas. Data from one male (freshly collected Oklahoma

species) and one female suggested that these animals may be capable of sustaining anaerobic speeds for long periods.

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References

Anderson, J. F. and Prestwich, K. N. (1985). The physiology of exercise at and above maximal aerobic capacity in a theraphosid (tarantula) spider, *Brachypelma smithi* (F.O. Pickard-Cambridge). *Journal of Comparative Physiology B* **155,** 529-539.

Anderson, J. F. and Prestwich, K. N. (1982). Respiratory gas exchange in spiders. *Physiological Zoology* **55,** 72-90.

Autumn, K., Jindrich, D., DeNardo, D. and Mueller, R. (1999). Locomotor performance at low temperature and the evolution of nocturnality in geckos. *Evolution* **53,** 580-599.

Beaupre, S. J. (1993). An ecological study of oxygen consumption in the mottled rock rattlesnake, *Crotalus lepidus lepidus*, and the black-tailed rattlesnake, *Crotalus molossus molossus,* from two populations. *Physiological Zoology* **66,** 437-454.

Beaupre, S. J., Dunham, A. E. and Overall, K. L. (1993). Metabolism of a desert lizard: the effects of mass, sex, population of origin, temperature, time of day, and feeding on oxygen consumption of *Sceloporus merriami*. *Physiological Zoology* **66,** 128-147.

Beaupre, S. J. and Duvall, D. (1998). Variation in oxygen consuption of the western diamondback rattlesnake *(Crotalus atrox)*: implications for sexual dimorphism. *Comparative Physiology* **168B,** 497-506.

Bennett, A. F. (1982). The energetics of reptilian activity. In *Biology of Reptilia*, vol. 13 (ed. C. Gans and F. H. Pough), pp. 155-199. London: Academic Press.

Bennett, A. F. and Dawson, W. R. (1976). Metabolism. In *Biology of Reptilia*, vol. 5 (ed. C. Gans), pp. 127-224. New York: Academic Press.

Brackenbury, J. H. and El-Sayed, M. S. (1985). Comparison of running energetics in male and female domestic fowl. *Journal of Experimental Biology* **117,** 349-355.

Chappell, M. A. (1983). Metabolism and thermoregulation in desert and montane grasshoppers. *Oecologia* **56,** 126-131.

Cullum, A. J. (1998). Sexual dimorphism in physiological performance of whiptail lizards (Genus *Cnemidophorus*). *Physiological Zoology* **71,** 54-552.

Foelix, R. (1996). Biology of Spiders, pp. 330. Oxford: Oxford University Press.

Ford, M. J. (1977). Metabolic costs of the predation strategy of the spider *Pardose amentat* (Clerck) (Lycosidae). *Oecologia* **28,** 333-340.

Full, R. J. (1987). Locomotion energetics of the ghost crab. I. Metabolic cost and endurance. *Journal of Experimental Biology* **130,** 137-153.

Full, R.J. and Herreid, C.F. (1983) The aerobic response to exercise of the fastest land crab. American Journal of Physiology **244,** R530-R536.

Full, R.J. and Weinstein, R.B. (1992). Integrating the physiology, mechanics and behavior of rapid running ghost crabs: slow and steady doesn't always win the race. American Zoologist **32**, 382-395.

Garland Jr., T. (1993). Locomotor performance and activity metabolism of *Cnemidophorus tigris* in relation to natural behaviors. In *Biology of whiptail lizards (Genus: Cnemidophorus)* (ed. J. W. Wright and L. J. Vitt), pp. 163-210. Norman: Oklahoma Museum of Natural History.

Gatten Jr., R. E., Miller, K. and Full, R. J. (1992). Energetics at rest and during locomotion. In *Environmental Physiology of the Amphibians* (ed. M. E. Feder and W. W. Burggren), pp. 314-377. Chicago: University of Chicago Press.

Greenstone, M. H. and Bennett, A. F. (1980). Foraging strategy and metabolic rate in spiders. *Ecology* **61,** 1255-1259.

Hamond, K.A., CHappell, M.A., Cardullo, R.A., Lin, R-S. and Johnsen, T. (2000). The mechanistic basis of aerobic performance variation in red junglefowl. *Journal of Experimental Biology* **203**, 2053-2064.

Herreid II, C. F. (1981). Energetics of pedestrian arthropods. In *Locomotion and Energetics in Arthropods.* (ed. C. F. Herreid II and C. R. Fourtner), pp. 491-526. New York: Plenum Press.

Herreid II, C. F. and Full, R. J. (1984). Cockroaches on a treadmill: aerobic running. *Journal of Insect Physiology* **30,** 395-403.

Humphreys, W. F. (1977). Respiration studies on *Geolycosa godeffroyi* (Araneae: Lycosidae) and their relationship to field estimates of metabolic heat loss. *Comparative Biochemistry and Physiology* **57A,** 555-563.

Jayne, B. C. and Bennett, A. F. (1990). Selection for locomotor performance capacity in a natural population of garter snakes. *Evolution* **44,** 1204-1299.

Lighton, J. R. B. (1985). Minimum cost of transport and ventilatory patterns in three African beetles. *Physiological Zoology* **58,** 390-399.

McQueen, D. J. (1980). Active respiration rates for the burrowing wolf spider *Geolycosa domifex* (Hancock). *Canadian Journal of Zoology* **58,** 1066-1074.

Miyashita, K. (1969). Effects of locomotory activity, temperature and hunger on respiratory rates of *Lycosa T-insignita* (Araneae: Lycosidae). *Applied Entomology and Zoology* **4,** 105-113.

Pate, R. R. & Kriska, A. (1984): Physiological basis for sex difference in cardiorespiratory endurance. *Sports Medicine* **1**, 87-98.

Paul, R. (1992). Gas exchange, circulation, and energy metabolism in Arachnids. In *Physiological Adaptations in Vertebrates: Respiration, Circulation, and Metabolism* (ed. S. C. Wood, R. E. Weber, A. R. Hargens and R. W. Millard), pp. 169-197. New York: Marcel Dekker, Inc.

Peakall, D. B. and Witt, P. N. (1976). The energy budget of an orb web-building spider. *Comparative Biochemistry and Physiology* **54A,** 187-190.

Prestwich, K. N. (1983). The roles of aerobic and anaerobic metabolism in active spiders. *Physiological Zoology* **56,** 112-132.

Pough, F.H., Magnusson, W.E., Ryan, M.J., Well, K.D. and Taigen, T.L. (1992). Behavioral energetics. In *Environmental Physiologoy of the Amphibians* (ed. M.E. Feder and W.W. Burggren), pp. 395-436. Chicago: University of Chicago Press.

Reinhold, K. (1999). Energetically costly behaviour and the evolution of resting metabolic rate in insects. *Functional Ecology* **13,** 271-224.

Rogowitz, G. L. and Chappell, M. A. (2000). Energy metabolism of eucalyptus-boring beetles at rest and during locomotion: gender makes a difference. *Journal of Experimental Biology* **203,** 1131-1191.

Sanborn, C. F. and Jankowski, C. M. (1994). Physiologic considerations for women in sport. *Clinical Sports Medicine* **13,** 315-327.

Schmidt-Nielsen, K. (1996). Animal Physiology: Adaptations and Environment, 5th edition. Cambridge, University of Cambridge Press.

Seymour, R. S. and Vinegar, A. (1973). Thermal relations, water loss and oxygen consumption of a North American tarantula. *Comparative Biochemistry and Physiology* **44A,** 83-96.

Snell, H. L., Jennings, R. D., Snell, H. M. and Harcourt, S. (1988). Intrapopulation variation in predator-avoidance performance of Galapagos lava lizards: the interaction of sexual and natural selection. *Evolutionary Ecology* **2,** 353-369.

Taigen, T.L., Emerson, S.B. and Pough, F.H. (1982). Ecological correlates of anuran exercise physiology. *Oecologia* **52,** 49-56.

Taylor, C. R. and Heglund, N. C. (1982). Energetics and mechanics of terrestrial locomotion. *Annual Review of Physiology* **44,** 97-107.

Taylor, C. R., Heglund, N. C. and Maloiy, G. M. O. (1982). Energetics and mechanics of terrestrial locomotion. I. Metabolic energy consumption as a function of speed and body size in birds and mammals. *Journal of Experimental Biology* **97,** 1-27.

Taylor, C. R., Schmidt-Nielsen, K. and Raab, J. (1970). Scaling of energetic cost of running to body size in mammals. *American Journal of Physiology* **219,** 1104-1107.

Walton, M. B., Peterson, C. C. and Bennett, A. F. (1994). Is walking costly for anurans: The energetic cost of walking in northern toad *Bufo boreas halophilus. Journal of Experimental Biology* **197,** 165-178.

Weinstein, R., B. and Full, R. J. (1998). Performance limits of low-temperature, continuous locomotion are exceeded when locomotion is intermittent in the ghost crab. *Physiological Zoology* **71,** 274-284.

Weinstein, R. B. and Full, R. J. (1999). Intermittent locomotion increases indurance in a gecko. *Physiological and Biochemical Zoology* **72,** 732-739.

Wells, C. L. & Plowman, S. A. (1983). Sexual differences in athletic performance: biological or behavioral? *Physician Sports medicine* **11,** 52-63.

Withers, P.C. (1977). Measurements of $\dot{V}_{O_2}$, $\dot{V}_{CO_2}$ and evaporative water loss with a flow-through mask. *Journal of Applied Physiology* **42**, 120-123.

Table 3.1: RMR, $\dot{V}_{CO_2}$ and linear regression statistics for the relationship between speed and V_{CO_2} in individual tarantulas. Bolded numbers at the end of columns indicate the means for the column.

Mass (g)	RMR ($\mu l\ CO_2\ h^{-1}$)	$\dot{V}_{CO_2max}$ ($\mu l\ CO_2\ h^{-1}$)	MAS ($m\ h^{-1}$)	Factorial Scope	Slope (C_{min}) ¶ ($\mu l\ CO_2\ m^{-1}$)	y – intercept¶ ($\mu l\ CO_2\ h^{-1}$)	y-intercept /RMR	r^2
Males								
9.35	156.1	2486.85	73.44	15.93	38.25 ± 2.82	-308.83 ± 154.27	-1.98	0.98
6.80	195.5	1432.66	73.44	7.33	7.02 ± 0.88	925.36 ± 43.12	4.73	0.97
5.39	139.2	1312.95	55.44	9.43	16.48 ± 6.29	300 ± 267.59	2.16	0.77
5.02	131.2	1060.42	55.44	8.08	20.83 ± 11.86	-165.68 ± 555.53	-1.26	0.75
9.23	204.2	1882.95	46.80	9.22	9.01 ± 1.51	1356.19 ± 64.33	6.64	0.94
5.68	116.2	1722.62	73.44*	14.82	19.51 ± 1.17	319.97 ± 59.00	2.75	0.99
6.91	**157.07**	**1650.24**	**63.00**	**10.80**	**18.52**	**404.50**	**2.17**	
Females								
18.90	183.5	2323.17	55.44*	12.54	51.48 ± 1.32	-539.06 ± 61.78	-2.94	0.99
17.55	296.1	2899.30	73.44	9.79	34.45 ± 2.93	324.81 ± 160.47	1.09	0.98
9.52	100.1	2556.22	80.64	25.53	23.09 ± 4.32	530.36 ± 262.78	5.29	0.91
17.20	207.6	3162.01	55.44	15.23	31.48 ± 8.08	1275.27 ± 343.66	6.14	0.88
14.07	192.0	1392.64	36.36*	7.25	-	-	-	-
17.90	237.4	1472.28	55.44*	6.20	21.12	301.32	1.26	-
15.72	**208.78**	**2300.94**	**59.46**	**12.75**	**32.32**	**378.54**	**2.17**	

¶ values include standard error of the slope and intercept
* individuals that reached anaerobic speeds

Table 3.2: Mass and cost of transport (C_{min}) for individual male and female tarantulas and their mean (± S.E.M.). Units for C_{min} are reported as mass-specific ml O_2 g^{-1} km^{-1}.

	Mass (g)	C_{min} (ml O_2 $g^{-1}km^{-1}$)
Females:	18.90	2.96
	17.55	2.13
	9.52	2.64
	17.20	1.99
	14.07	-
	17.90	1.28
Mean	**15.72 ± 1.43**	**2.2 ± 0.65**
Males:		
	9.35	4.45
	6.80	1.15
	5.39	3.32
	5.02	4.59
	9.23	1.06
	5.68	3.65
Mean	**6.91 ± 0.78**	**3.04 ± 0.70**

Table 3.3: ANCOVA results for comparisons of $\dot{V}_{CO_2}$ (ml h^{-1}) of male and female tarantulas (A. anax) at different speeds. Body mass is a covariate of $\dot{V}_{CO_2}$.

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

Values are means ± S.E.M.

Table 3.4: $\dot{V}_{O_2max}$ (in mass-specific units), factorial scope and MAS for three species of female tarantulas at similar temperatures (23 – 25 °C). For comparison, $\dot{V}_{CO_2max}$ measured in this study was converted to ml O_2 h^{-1} using an RQ of 0.92. The MAS reported in the table for this study is the highest MAS measured.

Mean Mass (g)	$\dot{V}_{O_2max}$ (μl O_2 $g^{-1}h^{-1}$)	MAS (m h^{-1})	Factorial Scope	
15.72	159.09	80.64	12.75	A. anax, this study
12.7	190	210	5	unknown species, Herreid, 1981
26.92	170	180	7.73	B. smithi, Anderson and Prestchich, 1985

Table 3.5: Comparison of C_{min} for male and female A. anax measured in this study with equations determined from interspecific arthropod data (Lighton 1985) and interspecific vertebrate and invertebrate data (Gatten et al. 1992). The C_{min}-mass scaling equation from Gatten et al. (1992) is reported in J kg^{-1} m^{-1}. C_{min} for a 6.91-g male and a 15.72-g female tarantula was determined first in J kg^{-1} m^{-1} and then converted to ml O_2 $g^{-1}km^{-1}$ using RQ = 0.92 and Joule-CO_2 coefficients from Nagy and Gessman (1988). An additional comparison for females is included from Herreid (1981), who measured C_{min} for an unknown species of female tarantula.

C_{min} (ml O_2 $g^{-1}km^{-1}$)	Source
Females	
(mass = 15.72g)	
2.20	empirical, this study
2.08	predicted, Lighton, 1985
1.88	predicted, Gatten et al., 1992
0.43	empirical, Herreid, 1981; C_{min} for 12.7 g female tarantula(species unknown)
Males	
(mass = 6.91g)	
3.04	mpirical, this study
2.67	predicted, Lighton, 1985
2.51	predicted, Gatten et al., 1992

List of Figures

least-squares regression line, is $C_{min} = 5.57\ M^{-0.37}$ ($r^2 = 0.16$), where M is body mass in grams.

FIGURE 3.1: Active MR versus speed for females.

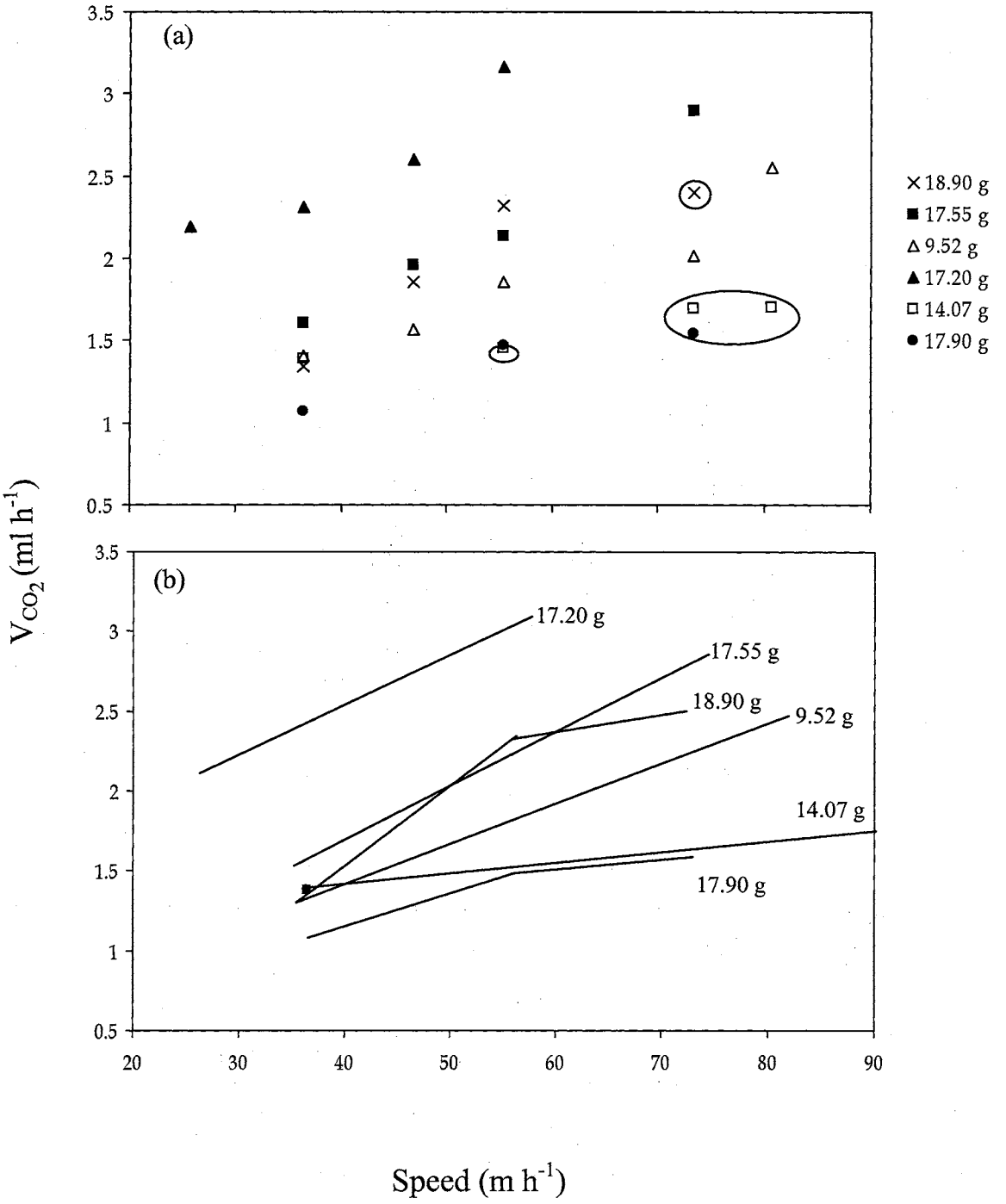


FIGURE 3.2: Active MR versus speed for males.

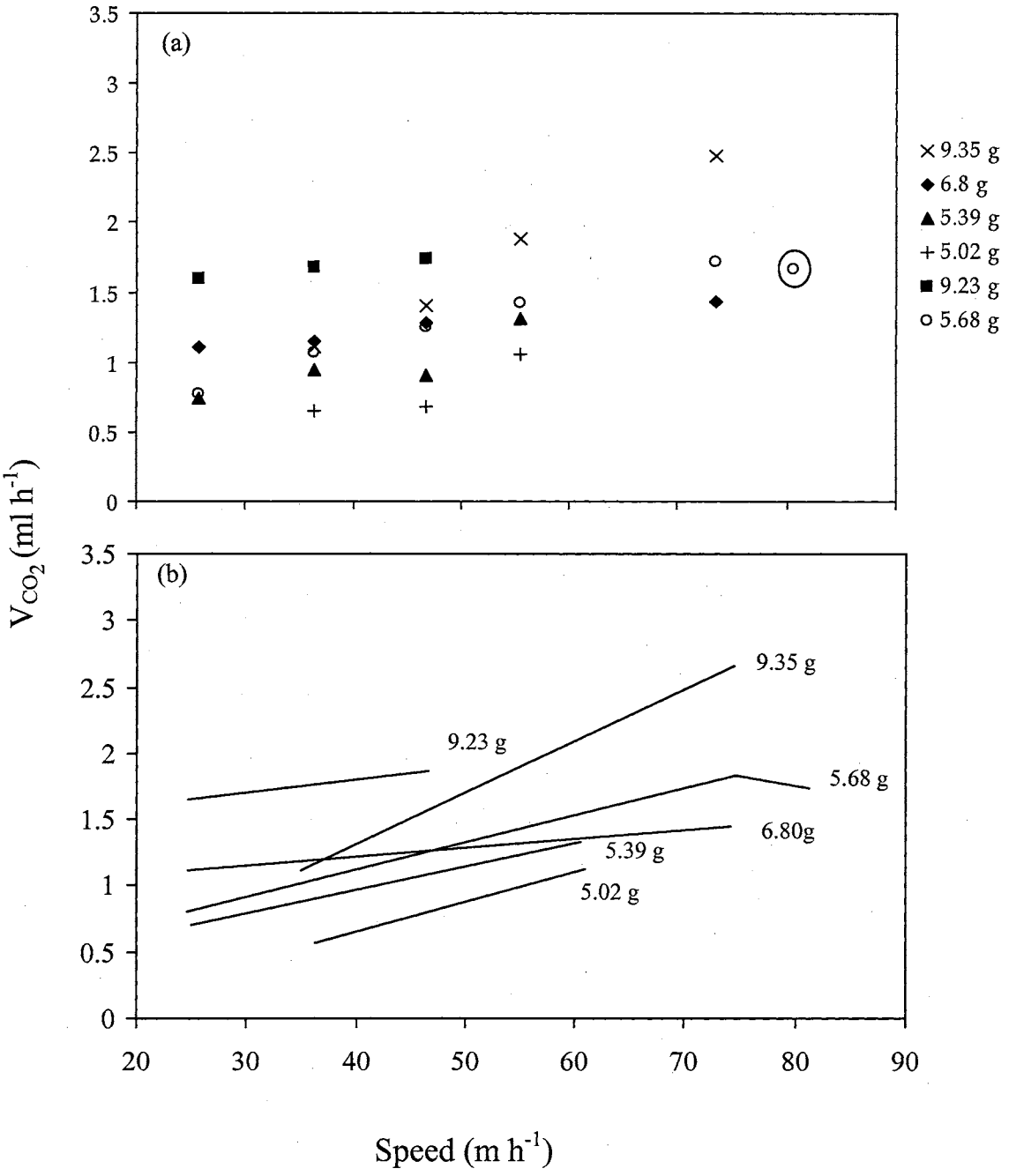
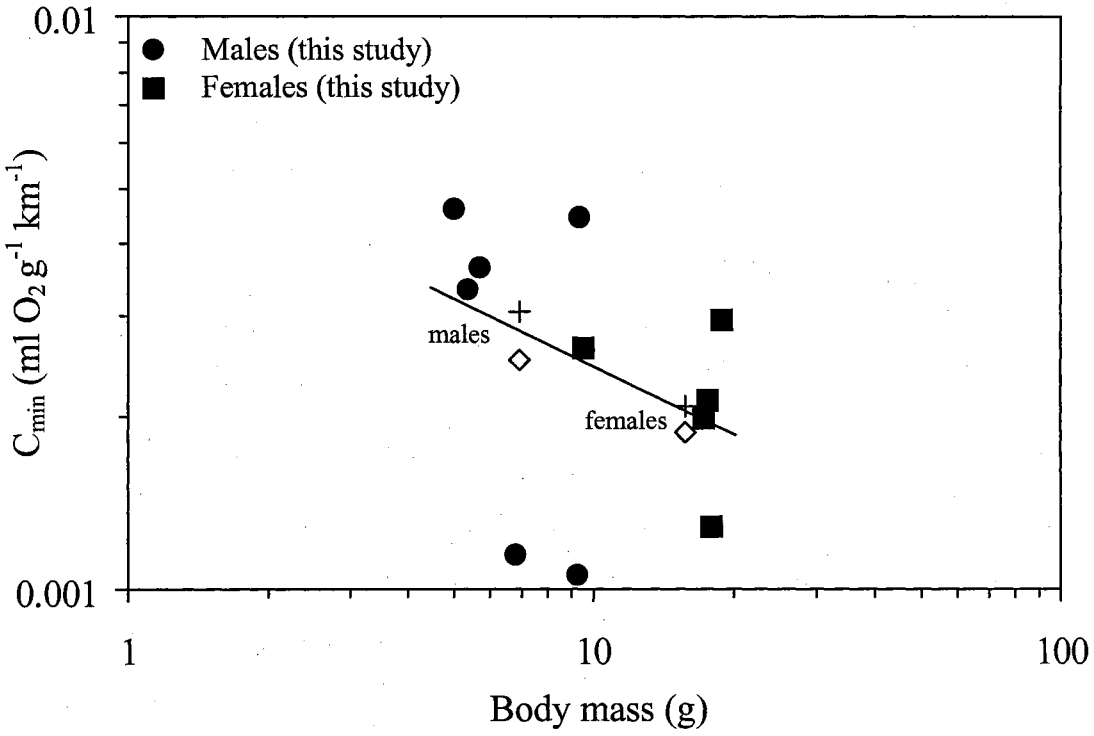


FIGURE 3.3: Minimum cost of transport for males and females.



2

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