Thermal ecology of male tarantulas (Aphonopelma anax) during the mating season

C. Shillington

Abstract: During the mating season, male tarantulas 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 ($T_b$) of active male tarantulas (Aphonopelma anax) encountered fortuitously in the field ranged from 24.7 to 35.1°C and preferred $T_b$'s measured in a laboratory thermal gradient ranged from 22.1 to 31.3°C. The thermal options available to males at random points in their environment varied substantially throughout the day but temperatures typically exceeded 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 environmental temperatures were within their preferred $T_b$ range at night and so active regulation of $T_b$ was unnecessary. In addition, I determined the exact times that males ceased locomotory activity in the morning (retreat) and when they started activity in the evening (emergence). Data from 23 radio-tagged males indicated that they retreated into temporary burrows between 06:47 and 10:53 CST. Activity commenced again between 16:36 and 20:53 CST as temperatures approached their preferred or selected $T_b$ range.

Résumé: Durant la saison de la reproduction, les tarentules (Aphonopelma anax) mâles quittent leur terrier et partent à la recherche de femelles qui sont très dispersées et qui demeurent dans leur terrier. Le mâles sont donc exposés à des fluctuations de plus grande ampleur des conditions du milieu sans avoir accès à un refuge permanent. La température du corps ($T_b$), mesurée chez des mâles actifs rencontrés au hasard en nature, se situe entre 24,7 et 35,1°C et la température $T_b$ préférée, déterminée en laboratoire le long d’un gradient thermique, va de 22,1 à 31,3°C. Les options thermiques offertes aux mâles à des points choisis au hasard dans leur environnement varient de façon importante pendant toute la journée, mais, de façon générale, se situent au-dessus de 40°C. Par comparaison, les températures dans les terriers demeurent en-deçà de 40°C. Les indices calculés à partir de ces données semblent démontrer que les mâles font une thermorégulation active durant le jour et qu’à la nuit, les températures du milieu se situent dans l’étendue des $T_b$ préférées et la thermorégulation active est alors superflié. J’ai déterminé, en outre, les moments exacts de cessation des déplacements le matin (enfouissement) et de reprise de l’activité locomotrice le soir (émergence). Les données recueillies chez 23 mâles marqués indiquent qu’ils regagnent leur terrier entre 06:47 et 10:53 (heure normale du Centre). L’activité reprend entre 16:36 et 20:53, alors que la température du milieu s’approche du registre des températures choisies et préférées.

[Traduit par la Rédaction]

Introduction

In ectotherms, biological processes are dependent either directly (by changing rates of biological reactions) or indirectly (e.g., costs of thermoregulation) on body temperature ($T_b$), which in turn depends on environmental temperature. Many ectotherms live in thermally variable environments, so their $T_b$ is also subject to variation. 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 (behavioral and (or) physiological) by which animals attempt to maintain their $T_b$ as close as possible to some preferred $T_b$ range (Hertz et al. 1993). Thus, the extent to which ectotherms thermoregulate reflects a combination of associated costs and benefits (Huey and Slatkin 1976; Shine et al. 2000).

Although the ability to regulate $T_b$ (thermoregulation) is well documented in a variety of vertebrate and invertebrate ectotherms (reviewed in Heinrich 1981; Avery 1982; Peterson 1987; Peterson et al. 1993), spiders as a group have received comparatively little attention. Spiders have been shown to regulate $T_b$ via behavioral mechanisms. These include orientation (mostly orb weavers) (Carrel 1978; Casey 1981; Cloudsley-Thompson 1991, 1993), changing position within a burrow (fossorial spiders) (Baerg 1958; Seymour and Vinegar 1973; Humphreys 1974, 1978; Minch 1978; 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; Punzo and Jellies 1983; Pulz 1987). In addition, spiders have been shown to select retreat sites according to the thermal properties of the environment (Riechert and Tracy 1975;
Male tarantulas of North America represent an interesting case for studying thermoregulation because of changes in life history that occur once sexual maturity is attained. As juveniles and subadults, both males and females are fossorial, sit-and-wait predators. Females remain fossorial throughout their lives and may inhabit the same burrow for many years, maybe even their entire lives (approximately 20 years) (Baerg 1958). However, once males reach sexual maturity, they abandon their burrows and actively search for widely dispersed females (Thornhill and Alcock 1983; Shillington and Verrell 1997). Movement during this time appears to be 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. For males in the wild, however, this period is probably much shorter, on average, because of exposure to predators and sexual cannibalism. Additionally, although males restrict their search activity to the cooler parts of the day (Minch 1978; Punzo and Henderson 1999), they are probably exposed to larger fluctuations in environmental conditions than females and, without the protection of a permanent burrow, are vulnerable to heat stress and desiccation (Seymour and Vinegar 1973; Punzo 1991; Janowski-Bell and Horner 1999). Janowski-Bell and Horner (1999) reported a continual loss of body mass in male tarantulas throughout the summer mating season, probably because of a combination of dehydration and decreasing energy reserves. Although male tarantulas will capture and consume fortuitously encountered prey while searching for females (personal observation), their total energy output over the season is likely greater than the input, resulting in a shorter life-span than that of sedentary females. The actual longevity of sexually mature males has not been recorded under natural conditions.

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 (both seasonal and circadian) has been 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 is usually a response to specific environmental conditions and may be related to the organism’s physiological adaptations.

Using a species of tarantula (Aphonopelma anax) found in southern Texas, I used the conceptual framework proposed by Hertz et al. (1993) to describe thermoregulation by males during the mating season and also to examine temporal patterns of emergence from and retreat into burrows. To do this, I measured (i) $T_b$ of active males, (ii) available thermal options (i.e., operative temperatures; see Porter and Gates 1996; Bakken 1981, 1992), and (iii) the $T_c$ 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 tarantulas are ideal subjects for ecological and behavioral studies because of their large size and seasonal activity, they remain a poorly studied group of animals. In this study I attempt to quantify some of the ecophysiological aspects that relate directly to male activity during the mating season (which may in turn influence fitness). This is not only critical to understanding tarantula ecology, but provides an excellent opportunity for studying general questions of sexual selection and thermal biology.

**Methods and materials**

**Study area**

During May–July of 1998–2000, fieldwork was conducted at the Chaparral Wildlife Management Area (CWMA), which is located approximately 13 km west of Artesia Wells, Texas. This 6150-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.) (for additional details see Hellgren et al. 2000). Male A. anax are active at this site from late May to late June, a period that typically coincides with peak rainfall events. Male activity decreases toward the end of June as 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 free-ranging animals encountered while road cruising. At each encounter with free-ranging males, (i.e., not captured in drift-fence buckets), I measured three different temperatures with a 30-gauge copper–constantan thermocouple connected to a digital thermometer: (1) $T_b$ (measured on the pedicle between the cephalothorax and the 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 internal temperature of the thorax is usually taken as a measure of $T_b$. However, measuring the 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; see below), therefore I hypothesized that an external measurement made directly on the thin pedicle between the cephalothorax and the abdomen would be a good indicator of internal cephalothorax $T_b$. Initial comparisons of internal and external $T_b$’s indicated no difference between the two types of measurements ($T_{b\text{-internal}}$ range = 25.5–31.6°C; $T_{b\text{-external}}$ range = 25.4–31.8; mean difference = 0.1°C; $n = 28$, paired $t$ test, $t = -0.91$, $p = 0.37$). Consequently, all further $T_b$’s were measured externally.

**Selected range of $T_b$’s**

I measured the selected range of $T_b$’s ($T_{b\text{adj}}$) in the laboratory in a 1.5-m linear thermal gradient using six randomly selected males. The gradient was maintained 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 to 46°C and fluorescent ceiling lights provided a 14 h light: 10 h dark photoperiod. I implanted a lightweight (30-gauge) copper–constantan thermocouple in each male’s cephalothorax and recorded \( T_b \) on a datalogger (Hobo Type T Thermocouple H12–003, Onset Computer Corporation). Males were given a 1-h acclimation period after which individual \( T_b \) was recorded every 10 min for a 24-h period. Observations of the activity of implanted and non-implanted male tarantulas suggested that the implanted thermocouple did not affect their behavior.

There is currently no standardization of methods for calculating \( T_{ad} \) from laboratory thermal gradients and investigators have used the central 50% (Hertz et al. 1993; Kearney and Predavec 2000), the central 80% (Diaz 1994; Bauwens et al. 1996), or the entire range of \( T_b \)’s (Punzo 1991; Rummery et al. 1994). I estimated \( T_{ad} \) as the central 80% of all \( T_b \)'s selected in the thermal gradient because this range included most major peaks in the frequency distribution of \( T_b \)'s.

**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 in position with its sensory tip in the middle of the hollow cephalothorax region. I measured temperatures using a digital thermometer and (or) dataloggers (Hobo Type T Thermocouple H12–003). I moved one model randomly through the environment and measured the temperature of this exoskeleton model (\( T_e \)) at random locations. After each \( T_e \) measurement I determined a new location by spinning the dial of a compass randomly to generate a new direction. The distance (number of paces) between successive locations was determined by starting and stopping a stopwatch randomly (1 s = one step). \( T_e \)'s were generated in such a manner through the entire field season and covering all hours from sunrise to sunset during June 2000 (6:43–20:41 CST). In addition, I measured \( T_e \) at half-hour intervals in the two most extreme microhabitats above ground, full sun and full shade, and I assumed that tarantulas that were active on the surface could achieve \( T_e \) anywhere between these two extremes. Models were left in the same location for 24-h periods to determine temperatures during a typical day and night. In 1999 and 2000, full-sun and full-shade measurements were obtained once a week during June, 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 over a 24-h period during both years in four burrows/refuges previously occupied by radio-tagged males.

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 sunlight. A live tarantula with an implanted thermocouple was free to move in the same area. Temperatures were recorded at 10-min intervals for approximately 6 h. Comparisons of model and tarantula during these times showed a mean difference of 0.16°C, and temperature measurements did not differ significantly from each other (\( n = 34; t \) test, \( t = -1.81, p > 0.08 \)). In the morning, \( T_b \) of the live animal tended to be lower than the exoskeleton model, but in the evening, the model \( T_b \) was lower. These differences suggested that rates of heat loss and heat gain were slightly higher in the model, presumably because the thermal inertia of the hollow exoskeleton was lower than the live animal. Overall differences between the exoskeleton and live animal were slightly higher in the evening than in the morning. The correlation between the two measurements was high (\( r = 0.994, p < 0.001 \)), suggesting that the exoskeleton model was a good indicator of tarantula \( T_b \).

**Thermoregulation indices**

I evaluated thermoregulation using 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 dataset with \( T_b \)'s from all the animals. The index \( d_b \) indicates the extent to which tarantulas experience \( T_b \) outside of \( T_{ad} \) and was calculated as the mean absolute deviation between \( T_b \) and the extremes of the \( T_{ad} \) range. The index \( d_b \) is an indication of the thermal quality of the habitat and was calculated as the mean absolute deviation between \( T_e \) and \( T_{ad} \). When \( T_b \) or \( T_e \) was within \( T_{ad} \), a deviation of zero was assigned. Finally, to address the question of how carefully tarantulas thermoregulate, I calculated an index of effectiveness (\( E \)): \( E = 1 - (d_b/d_e) \). An \( E \) value close to zero indicates no thermoregulation, while values closer to 1 suggest increasingly 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 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, 1998–1999; ~0.65 g Holohil, 2000). These were glued to the posterior portion of the carapace after some of the hairs and dirt were removed with rubbing alcohol. I released these animals close to their sites 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 daily and measured \( T_b \) during activity on alternate days to minimize disturbance to the animals. During 1999 and 2000, I relocated individual males for 2 consecutive days approximately every 2 h while they were active. In the mornings, I maintained visual contact with these radio-tagged animals and recorded the exact time when males ceased activity and retreated into daytime refuges. I simultaneously recorded air and substrate temperatures, relative humidity, and light intensity (Hobo-H8 temperature/relative humidity/light intensity data logger). In the evening I waited beside these refuges and recorded the exact time males left their temporary daytime refuges. Activity was often preceded by a period of alertness or movement within the burrow, but the time of emergence was only recorded once animals left the refuge. Again I recorded air and substrate temperatures, relative humidity, and light intensity at the exact time when males emerged from their refuges. I tested the data for correlations between time and the corresponding environmental variables to determine if choice of retreat and
emergence times were associated with changes in temperature, light level, and humidity.

Results

Body temperature
I encountered a total of 96 active adult tarantulas over the 3 summers (not including females found in burrows). Of these, 86 were males (89.6%) and 10 were females (10.4%). There was no difference between males and females in Tsel’s measured (Kruskal–Wallis test, χ² = 0.912, p = 0.76); however, because of the small sample size for females, all subsequent analyses are for males only. From 58 of these free-ranging males I obtained a total of 128 Tsel measurements that ranged from 24.7 to 35.1°C, with a mean of 29.4°C (Fig. 1a).

The majority of Tsel measurements (including both fortuitously encountered 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 differences between Tsel (at tarantula level),Tem, and Tsep measurements that were recorded sequentially within 2 min 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, Tsel fell between Tem and Tsep (mean Tsel = 28.6, mean Tem = 29.1, mean Tsep = 29.3).

Selected range of Tsel’s
Tsel of six male tarantulas was measured over a 24-h period in the thermal gradient. The voluntary thermal maximum (VTmax) was 35.1°C, and across all tarantulas Tsel’s ranged from 18 to 35.1°C (Fig. 1b). I discarded data from one animal because he remained at the cold end of the gradient for the entire experimental period and exhibited little movement. All other males appeared to move randomly within the gradient for the entire 24-h period, with no evidence of a nocturnal/diurnal pattern. I estimated Tsel as the central 80% of all Tsel’s selected because this range included most major peaks in the frequency distribution of Tsel’s (Fig. 1b). So defined, Tsel ranged from 22.1 to 31.3°C.

Operative temperatures
Operative temperatures during the day reached maximal ranges between 11:00 and 18:00 CST (Fig. 2). The temperatures of hypothetical male tarantulas moving randomly throughout the environment (Te-random) are shown in Fig. 2 along with possible high and low extremes (full sun (Te-sun) and full shade (Te-shade)). In addition, temperatures available to inactive males remaining in burrows during the same period are shown (Tb burrow). The values for Te-shade, Te-sun, and Tb burrow are means for each half-hour period, based on a total of eight measurements (four from each year). The mean and range of temperatures for each temperature variable varied substantially (Table 1). 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 (Te-sun), reached a maximum temperature of only 63.2°C. Most of the variation in Te-sun during daytime hours (Fig. 2) can be attributed to intermittent cloud cover (personal observation). Te-random deviated widely from Tsel, and only 16.5% of all Te-random measurements were within Tsel (Fig. 1c).

Te-shade and Tb burrow stayed stable throughout the day. The Tb burrow range was less than 10°C, compared with ranges of more than 20°C in the other microhabitats (Table 1). In addition, Tb burrow measurements were similar to Tsel determined in the laboratory thermal gradient and were seldom above VTmax. All operative temperatures measured at night were within Tsel, and Te measurements taken in the two extreme environments indicated that a completely sunny thermal environment deviated, on average, 16.9°C above VTmax. During daylight hours (approximately 10:30–19:30 CST), Te-sun was above VTmax for 68% of the time. Te-shade values were above VTmax between 11:30 and 14:00 CST by an average of 3.87°C.

Thermoregulation indices
The index ds was determined from Tem measurements obtained by moving an exoskeleton model randomly throughout the environment and Tsel. Although the lower limit of Tsel was 22.1°C, Tem at the field site never fell below 23°C during this study. In addition, because nocturnal temperatures always remained within Tsel, ds is defined as zero and the effectiveness of thermoregulation (E) is undefined for this time period. I therefore restricted further analysis to data collected between sunrise and sunset.

During the daytime, ds was low (Table 2), which indicated that Tsel’s of active males closely matched Tsel; i.e., they seldom experienced temperatures outside the selected Tsel range determined in the thermal gradient. The ds values calculated during the 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 Tsel. Not surprisingly, E values indicated that males thermoregulated carefully (Table 2).

However, when I further partitioned the day and analyzed data only from times when tarantulas were active (morning and evening), a somewhat different pattern was revealed (Table 2). When recalculated, ds did not change significantly (Tsel’s closely matched Tsel), but ds indicated that the average thermal quality of the habitat was relatively high in the mornings, i.e., Tem was close to Tsel (low ds value), compared with the evenings (high ds value). As a result, males did not thermoregulate as carefully (E = 0.77) in the morning as in
the evening ($E = 0.95$). $T_b$'s were close to $T_{sel}$ in the evening even though $T_e$'s were more often outside $T_{sel}$.

Emergence and retreat of radio-tagged males

Of the 23 radio-tagged males, 3 lost their radio tags, 5 were eaten by roadrunners ($Geococcyx$ californianus) (personal observation), and 1 was eaten by a female tarantula after successfully mating with her (successful matings without cannibalism were also observed on three occasions). I determined that males commenced activity between 16:36 and 20:53 CST (mean = 19:32 CST). Emergence before 19:00 occurred only on overcast days.

Once they had emerged from daytime refuges, males remained active for the entire night. After sunrise, they retreated into new daytime refuges between 06:47 and 10:53 CST (mean = 08:59 CST). No male was ever observed returning to the same daytime refuge. Typical refuges were underground burrows of various sizes and depths (possibly abandoned rodent burrows). On four occasions when it was completely overcast and (or) raining for the entire day, males remained above ground and sometimes climbed up available vegetation (mesquite trunks or tasajillo stems) instead of retreating underground. $T_a$ on these days did not exceed 40°C.

Retreat and emergence times and their associated environmental variables ($T_a$ and $T_s$, relative humidity, and light intensity) were analyzed separately. As stated previously, tarantula $T_b$’s were not significantly different from either $T_a$ or $T_s$ and usually fell between these two variables. I calculated a mean value ($T_{env}$) from $T_a$ and $T_s$ and this was used in correlation analyses. Trends in correlations were similar on days 1 and 2, so data from both days were pooled (Fig. 3). If males retreated between sunrise and 10:53 CST and environmental variables did not affect retreat times within that period, then it was predicted that increasing temperature and light levels would be positively associated with time, i.e., a
positive correlation. Alternatively, humidity levels were expected to decrease with time in the morning (negative correlation). The retreat data and correlations (Fig. 3) suggest that the predicted patterns were confirmed: males that were active for longer in the morning experienced both 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 a daytime refuge before $T_{env}$ exceeded the VT max of 33°C (mean = 29.4°C, range = 24.1–37.5°C) and while the relative humidity was above 40%.

For evening emergence times, the relationship between humidity and time is more complex because around sunset (20:31 CST) the humidity starts to rise after reaching a daytime low between 16:00 and 20:00 CST. This time period coincided with emergence of males, which explained some of the variability in relative humidity despite the negative correlation ($r = -0.50$, $p = 0.01$) (Fig. 3). The predicted pattern of temperatures and light intensities was the reverse of what occurred in the morning (i.e., a negative correlation with time was predicted). Time of emergence showed a predicted 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. 3). However, time of emergence did not show the predicted negative correlation (indicating no effect of temperature on time of emergence) 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 $T_{env}$'s were within some suitable range that was independent of time. This is further supported by the narrow $T_b$ range (29.1–38.8°C) experienced by males when they emerged from their daytime refuges, a range that is independent of time. Only two individuals had emergence $T_b$'s that were above VT max (35.1°C) and these occurred late in the day on especially hot days, again suggesting that males were delaying their emergence until slightly lower environmental temperatures were reached.

**Discussion**

Male tarantulas at the CWMA were predominantly nocturnal. During the night, thermoregulation was unimportant because $T_{env}$ 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. 2). These patterns of temperature availability can be used to explain temporal activity patterns described for male *A. anax* (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 $T_{sel}$ be-
fore emerging. Temperature variation affects both metabolic rates and water loss in these tarantulas, with higher temperatures leading to increased metabolic rates and higher rates of water loss (Shillington 2001).

A critical thermal maximum (CTM) of approximately 43°C (varies slightly with acclimation temperature) has been determined for two *Aphonopelma* species: *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 good approximation of CTM for the male *A. anax* used in this study because habitat and daily temperature ranges are similar for all three species. Based on this value, daytime temperatures in full sun are probably well beyond the upper critical limits for these animals and even *T*<sub>shade</sub> (above ground) approached critical limits. Thus, the thermal environment surely restricts the diurnal locomotory activities of male tarantulas.

**Thermoregulation indices**

*T*<sub>sel</sub> for males spanned a relatively wide range (Fig. 1b), which 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 min during the entire 24-h period. For mature males, locomotory activity is probably more important for mating success than careful selection of *T*<sub>bl</sub>, resulting in a broad *T*<sub>bl</sub> range. Shine et al. (2000) suggest a similar lack of precise *T*<sub>bl</sub> 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. Combining behavioral observations with these data provides 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 most likely to occur when males emerged well before sunset, when *T*<sub>a</sub> and *T*<sub>s</sub> were still relatively high, suggesting that temperature may have influenced this behavior. Thus, for these animals effective thermoregulation was achieved by finding and remaining within a thermally suitable retreat. Once they were active, however, nighttime environmental temperatures were within *T*<sub>sel</sub> so the males had no need to thermoregulate.

In the morning, the thermal quality of the habitat was typically closer to *T*<sub>sel</sub> (low *d*<sub>0</sub> 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 toward 10:30 CST as *T*<sub>a</sub> and *T*<sub>s</sub> increased quickly above *T*<sub>sel</sub>. Behaviors included retreating from sunny locations and (or) increasing
the rate of locomotion in sunny areas compared with shaded areas. However, rates of locomotion were not measured. Despite these behaviors, males appeared to be very particular in their 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 long stretches of open, unshaded areas in search of additional burrows. Toward 10:00 CST, these unshaded areas represented thermally stressful habitat (Fig. 2) and were typically avoided by males, although they would occasionally tolerate the high temperatures for short periods of time during their search for a suitable thermal refugium.

Emergence and retreat

Based on observed activity patterns, it appears that choice of a retreat site was more important than temperature in determining when males ceased activity, because many males retreated into burrows while temperatures were still well within $T_{opt}$. Although finding retreat sites during the day may be very important for males if they are to avoid heat stress and desiccation, thermally suitable retreats also increase the time spent at physiologically favorable $T_{th}$'s (i.e., a $T_{th}$ range at which ectotherms perform optimally) (Huey and Stevenson 1979; Huey et al. 1989; Schaub and Grigg 1998; Webb and Shine 1998). These more favorable $T_{th}$'s in turn affect physiological traits such as metabolic rate (Huey and Slatkin 1976; Bennett and Nagy 1977; Stevenson 1985; Huey 1991; Peterson et al. 1993). Males that found burrows where temperatures remained well below 40°C would have similar $T_{th}$'s and so would experience lower daytime metabolic rates (Punzo 1991), thus minimizing energy expenditure (Huey 1991; Beaupre 1995, Shillington 2001). 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 a reduced time of exposure to daytime predators such as roadrunners.

The costs associated with finding suitable burrows included time spent investigating many different burrows, which reduced time available for mate searching, as well as increasing energetic expenditure and thermal stress as tarantulas moved between shrub clumps and were exposed to solar radiation. Males that found a suitable retreat early in the morning and ceased activity may have reduced their chances of finding receptive females because their periods of mate-searching activity were shorter. 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 thermally suitable burrows.

Although my data suggest that temperature was the most limiting factor for male tarantula activity, I observed exceptions to this on several days when daytime temperatures remained in the high 30s throughout the day, owing to heavy cloud cover. Despite these moderate temperatures, males were still inactive during the middle part of the day. Minch (1978) and Punzo and Henderson (1999) reported that light intensity influences activity of female tarantulas. Thus, timing of activity patterns may be influenced by a combination of factors including a biological clock and several environmental variables such as light intensity, humidity, and predation.

Acknowledgements

Special thanks are extended to Charles C. Peterson for his suggestions, which greatly improved this project and the resulting manuscript. I thank D. Synatske and the CWMA for allowing access to the area and providing accommodations during the field component of this study. I also thank D. Ruthven III for being so willing to collect tarantulas and particularly R. Kazmaier for his help and suggestions with many aspects of this project. I also thank V. Hutchinson and D. Lutterschmitt for use of the thermal gradient and associated equipment. Finally, I gratefully acknowledge M. Ewing, S. Fox, J. Sauer, P. Verrell, B. McEwen, Dr. A. Pasquet, and an anonymous reviewer for their comments on the manuscript. This study was funded in part by grants from the American Arachnological Society and Sigma Delta Epsilon.

References


© 2002 NRC Canada


