Metabolic rates and movements of the male tarantula *Aphonopelma anax* during the mating season

T. Stoltey and C. Shillington

**Abstract:** Tarantulas exhibit sexual dimorphism in their resting metabolic rate (RMR). The significantly higher RMRs observed in sexually mature males may be an adaptive strategy to support their higher energetic demands when searching for females. In this study, we investigated how intrasexual differences in male RMR may affect their locomotory activity and behavior during the mating season. Over a 2-year period, we radio-tagged male Texas tan tarantulas (*Aphonopelma anax* (Chamberlin, 1940)), measured their movements, and periodically recorded their metabolic rates in an open-flow respirometry system over the course of the breeding season. Differences found in search speed, search-area size, and movement patterns were not sufficiently explained by the small amount of intrasexual variation exhibited in RMR. Individuals were capable of searching areas up to 29 ha and moved up to 365 m/day. In addition, metabolic rate measured over a 24 h period showed no circadian periodicity and remained constant over the season. Lastly, the body condition of new captures stayed constant throughout the season, corroborating observations of males feeding and drinking.

**Résumé :** Les tarentules ont un dimorphisme sexuel de leur taux de métabolisme de repos (RMR). Les RMR significativement plus élevés observés chez les mâles matures sexuellement peuvent représenter une stratégie adaptative pour combler leurs besoins énergétiques accrus lors de la recherche de femelles. Nous examinons, dans notre étude, comment les différences intrasexuelles du RMR des mâles peuvent affecter leur activité et leur comportement locomoteurs durant la saison de reproduction. Sur une période de 2 ans, nous avons muni des mâles de la mygale brune du Texas *Aphonopelma anax* (Chamberlin, 1940) d’étiquettes radio, mesuré leurs déplacements et enregistré périodiquement leurs taux métaboliques dans un système de respirométrie en circuit ouvert au cours de la saison de reproduction. Les différences observées dans la vitesse de recherche, la taille de la surface de recherche et les patrons de déplacement ne sont pas suffisamment expliquées par la petite quantité de variation de RMR entre les sexes. Les individus sont capables de faire des recherches sur des surfaces pouvant atteindre 29 ha et se déplacent de jusqu’à 365 m/jour. De plus, le taux métabolique mesuré sur une période de 24 h ne montre aucune périodicité circadienne et demeure constant au cours de la saison. Enfin, la condition corporelle des nouvelles captures demeure constante au cours de la saison, ce qui corrobore nos observations sur l’alimentation et l’ingestion d’eau des mâles.

[Traduit par la Rédaction]

**Introduction**

The total amount of energy available to an ectotherm may be constrained physiologically (e.g., ability to process food; Karasov and Levey 1990; Peterson et al. 1990), ecologically (e.g., resource availability; Speakman 1999), or by thermal constraints on foraging time (Grant and Dunham 1988; Beaupre 1995). As a result, energy expenditures associated with activity, maintenance, growth, and reproduction may vary among and within individuals. Variation in these allocations may, in turn, restrict or stagger behaviors through time, thus affecting an individual’s life history and ultimately the general population properties of a species (Dunham et al. 1989; Beaupre and Duvall 1998; Shillington 2005). Although much of the variation observed in metabolic rate (MR) can be attributed to both body mass and ambient temperature (Kleiber 1932; Nespolo et al. 2003; Zaidan 2003; Dorcas et al. 2004), numerous correlations with life-history traits have been reported for different animal taxa (McNab 2002). These include locomotory patterns (Weinstein and Full 1998), mode of locomotion (Rogowitz and Chappell 2000), sex (Beaupre and Duvall 1998; Kotiaho 1998; Rogowitz and Chappell 2000; Shillington 2005), and interhabitat differences (Karasov and Anderson 1984).

Like many desert animals, spiders can survive prolonged periods of food scarcity by maintaining a low resting metabolism (Anderson 1974; Merkt and Taylor 1994; Lighton and Fielden 1995). A reduction in maintenance energy expenditure coupled with the ability to ingest large volumes of food enables spiders to survive long periods of limited prey availability and thus occupy niches and habitats where most other equally sized ectotherms would die of starvation (Itô 1964; Nakamura 1972; Anderson 1974; Humphreys 1977). These mechanisms are likely an evolutionary response to fluctuating prey densities and also occur in some snakes, which can survive periods of starvation exceeding 2 years (Anderson 1974; McCue 2007).

Tarantulas (Araneae: Theraphosidae) are sit-and-wait...
strategists that may remain in the same location for several years, traveling only a few metres from an established retreat to search for prey (Shillington and Verrell 1997; Yáñez and Floater 2000). When males become sexually mature (varies with species; >5 years for Texas tan tarantulas, Aphonopelma anax (Chamberlin, 1940)), they abandon both their established retreats and sedentary life styles. By this time, resting metabolic rates (RMRs) of mature males are significantly higher than those of sedentary females (Shillington and Peterson 2002; Shillington 2005) and they engage in high levels of sustained locomotory activity while searching for burrow-dwelling females. This scramble for mates does not involve combat or aggressive display (Shillington and Verrell 1997) and instead intrasexual competition is based predominantly on selection for better search abilities including locomotory performance, and thus mating success may largely depend on rapid walking (Schwagmeyer and Woontner 1986; Schwagmeyer 1988; Shillington 2002).

Mating occurrence has a major effect on a male tarantula’s energy budget. Male tarantulas travel farther during the breeding season than at any other period of their life cycle and die shortly thereafter (Baerg 1928, 1963; Minch 1978). Near the end of the breeding season, males of some North American species are reported to be lethargic and to have shrunken abdomens, a sign of depleted energy stores (Janowski-Bell and Horner 1999).

Locomotory ability is extremely important to male tarantulas during the breeding season and therefore they may adjust their behaviors to overcome physiological constraints and extend mate searching activities. Tarantula aerobic activity capacity is limited by an open circulatory system, inefficient book lungs, and copper-based respiratory pigment hemocyanin, which possesses an oxygen affinity lower than that of hemoglobin (Anderson and Prestwich 1982; Paul et al. 1989). As a result of these physiological constraints, males may maximize their locomotory performance through behavior. Behavior can be viewed as a potential filter between selection and performance (Garland et al. 1990; Garland and Losos 1994). Male movement has been observed to be interrupted by short pauses of inactivity (Shillington 2002). These pauses may indicate that males are utilizing intermittent locomotion, also called stop–go running (Miller 1979), to modify locomotory behavior (Kramer and McLaughlin 2001). By performing brief behaviors such as walking more frequently or increasing the number of pauses during movement, animals can minimize energy expenditure just as if they increased the duration of continuous behaviors (Edwards and Gleeson 2001). Frequent transitions from rest to locomotion have been shown to increase the total distance traveled before the onset of fatigue and therefore may enable individuals to increase the area searched for females (Weinstein and Full 1992, 1998, 1999; Kramer and McLaughlin 2001).

The aim of this study was to examine male locomotory performance during the mating season. Specifically, we addressed the following four questions. (1) Do male tarantulas with higher RMRs have higher rates of movement? (2) Do MRs and body condition change over the course of the breeding season? (3) Do patterns exist in movement (i.e., intermittent locomotion and directionality)? (4) How far do individuals travel and what areas are searched?

RMRs affect an animal’s activity capacity, which has been shown to be both heritable and highly variable in populations and thus susceptible to natural selection (Garland et al. 1990; Bennett 1991). If variations exist in RMR and locomotory performance among the males from this population, it may influence their survival and mating success. We predicted that (i) males with higher RMRs will have higher activity capacities and be able to search for females at faster rates; (ii) male MRs will decline over the course of the season as their energy stores are depleted; and (iii) males may use intermittent movement patterns to maximize locomotory performance.

Materials and methods

Research was conducted at the Chaparral Wildlife Management Area (CWMA) from 25 May to 6 July 2004 and from 4 June to 16 July 2005. The CWMA is a 6.15 ha research area located 13 km west of Artesia Wells, Texas, in an oak woods and prairie ecoregion that is divided into 15 fenced pastures of differing sizes and range management regimes. The area’s vegetation is largely dominated by honey mesquite (Prosopis glandulosa Torr.), acacia (genus Acacia P. Mill.), and Engelmann pricklypear cactus (Opuntia engelmannii Salm-Dyck) that form dense thickets often enclosing clearings of open tall grass pasture.

At this location, sexually mature male tarantula A. anax are active from late May until late July. They emerged from daytime refugia between 1636 and 2053 central standard time (CST) and were active until 0647–1053 CST (Shillington 2002). Males were collected on or alongside the roads that connected the pastures of the management area. After collection, individuals were taken back to the laboratory for further measurement (MR, carapace width, tibia length, mass) before being released after 2200 CST at their site of capture. Measurements of environmental temperature and absolute humidity were recorded using a data logger (Hobo Pro Series Temp, RH; Onset Computer Cooperation, Pocasset, Massachusetts, USA) attached to the base of a shaded mesquite tree trunk. Measurements of environmental temperature, retreat temperature, and absolute humidity were recorded using data loggers (Hobo Type T-1 Thermocouple; Onset Computer Cooperation). Analyses of variance (ANOVA) were used to compare temperature and humidity between years.

Radio-tracking and movement

Captured males weighing more than 7.0 g were fitted with radio transmitters ≤10% of body mass (0.64–0.99 g; Wildlife Materials, Murphysboro, Illinois, USA) and tracked using a Yagi antenna and TR-4 receiver (Telenics, Mesa, Arizona, USA) through the breeding season. Cyanoacrylate-based adhesive was used to affix the radio tag to the carapace of a male that was gently restrained on a foam block. Similar procedures were used in prior radiotelemetry studies with tarantulas (Janowski-Bell and Horner 1999; Shillington 2002). After the adhesive had cured, the tags were painted a dark brown, matching the color of the carapace to make them inconspicuous to predators. Radio-tagged males were then reweighed and released after 2200 CST at their site of capture. After 18–22 days, the radio tags were in danger of
losing battery power and thus all males were recaptured and refitted with a new radio transmitter. Transmitter removal could be accomplished only once without damaging the carapace of A. anax; therefore, males were able to be fitted with a maximum of two transmitters during the season.

The GPS (UTM-NAD27) location and behaviors of every radio-tagged male were observed and recorded at least once per night (2200–0600 CST) and once during the day (0600–1800 CST) throughout the study. ArcView version 3.3 and the Animal Movement extension were used to calculate daily distance (distance from the first observation of the day to the last observation of the day), total distance (sum of daily distances), search area, and direction of travel (compass bearing from true north). Search areas were estimated by measuring the area of the smallest convex polygon determined from a male’s outermost observation points (Losos and Gannon 1990). It is a conservative method that is dependent on sample size (Jennrich and Turner 1969; Giesen and Braun 1992). Total distance was divided by total time observed in the field (sum of days in the field) to calculate the overall rate of movement (m/day) during the breeding season. Movement data were tested for correlations using linear regression. Where necessary, data were first log10-transformed to reduce heteroscedasticity of variance. Male movement was tested for directionality using circular statistics calculated by the Animal Movement extension for ArcView version 3.3. Z values and sample sizes were used to calculate the probability level of rejecting the null hypothesis of directed movement using a Z table (Zar 1999).

In addition, every 2–5 days a minimum of one 30 min observation of movement and behavior was completed at night after 2200 CST. During each session, males were carefully followed from a distance of about 1 m and a flag was placed along its path at 5 min intervals to mark its progress. Behavioral data including pause duration(s), walk duration(s), substrate type, and body shaking were recorded using Ethoscribe analysis software (Tima Scientific, Inc., Sackville, New Brunswick, Canada) running on a hand-held computer (Newton MessagePad; Apple, Inc., Cupertino, California, USA). Pause and walk durations were compared within years using Wilcoxon’s rank signed tests and between years using Mann–Whitney rank sum tests because their distributions were not normal. Tarantulas have poor vision and cannot see beyond 2.5–5 cm (Baerg 1958); thus their distributions were not normal. Tarantulas have poor vision and cannot see beyond 2.5–5 cm (Baerg 1958); thus their distributions were not normal. Tarantulas have poor vision and cannot see beyond 2.5–5 cm (Baerg 1958); thus their distributions were not normal. Tarantulas have poor vision and cannot see beyond 2.5–5 cm (Baerg 1958); thus their distributions were not normal. Tarantulas have poor vision and cannot see beyond 2.5–5 cm (Baerg 1958); thus their distributions were not normal. Tarantulas have poor vision and cannot see beyond 2.5–5 cm (Baerg 1958); thus their distributions were not normal. Tarantulas have poor vision and cannot see beyond 2.5–5 cm (Baerg 1958); thus their distributions were not normal. Tarantulas have poor vision and cannot see beyond 2.5–5 cm (Baerg 1958); thus their distributions were not normal. Tarantulas have poor vision and cannot see beyond 2.5–5 cm (Baerg 1958); thus their distributions were not normal. Tarantulas have poor vision and cannot see beyond 2.5–5 cm (Baerg 1958); thus their distributions were not normal. Tarantulas have poor vision and cannot see beyond 2.5–5 cm (Baerg 1958); thus their distributions were not normal. Tarantulas have poor vision and cannot see beyond 2.5–5 cm (Baerg 1958); thus their distributions were not normal. Tarantulas have poor vision and cannot see beyond 2.5–5 cm (Baerg 1958); thus their distributions were not normal. Tarantulas have poor vision and cannot see beyond 2.5–5 cm (Baerg 1958); thus their distributions were not normal. Tarantulas have poor vision and cannot see beyond 2.5–5 cm (Baerg 1958); thus their distributions were not normal. Tarantulas have poor vision and cannot see beyond 2.5–5 cm (Baerg 1958); thus their distributions were not normal. Tarantulas have poor vision and cannot see beyond 2.5–5 cm (Baerg 1958); thus their distributions were not normal. Tarantulas have poor vision and cannot see beyond 2.5–5 cm (Baerg 1958); thus their distributions were not normal. Tarantulas have poor vision and cannot see beyond 2.5–5 cm (Baerg 1958); thus their distributions were not normal. Tarantulas have poor vision and cannot see beyond 2.5–5 cm (Baerg 1958); thus their distributions were not normal. Tarantulas have poor vision and cannot see beyond 2.5–5 cm (Baerg 1958); thus their distributions were not normal. Tarantulas have poor vision and cannot see beyond 2.5–5 cm (Baerg 1958); thus their distributions were not normal. Tarantulas have poor vision and cannot see beyond 2.5–5 cm (Baerg 1958); thus their distributions were not normal. Tarantulas have poor vision and cannot see beyond 2.5–5 cm (Baerg 1958); thus their distributions were not normal. Tarantulas have poor vision and cannot see beyond 2.5–5 cm (Baerg 1958); thus their distributions were not normal. Tarantulas have poor vision and cannot see beyond 2.5–5 cm (Baerg 1958); thus their distributions were not normal. Tarantulas have poor vision and cannot see beyond 2.5–5 cm (Baerg 1958); thus their distributions were not normal. Tarantulas have poor vision and cannot see beyond 2.5–5 cm (Baerg 1958); thus their distributions were not normal. Tarantulas have poor vision and cannot see beyond 2.5–5 cm (Baerg 1958); thus their distributions were not normal. Tarantulas have poor vision and cannot see beyond 2.5–5 cm (Baerg 1958); thus their distributions were not normal. Tarantulas have poor vision and cannot see beyond 2.5–5 cm (Baerg 1958); thus their distributions were not normal. Tarantulas have poor vision and cannot see beyond 2.5–5 cm (Baerg 1958); thus their distributions were not normal. Tarantulas have poor vision and cannot see beyond 2.5–5 cm (Baerg 1958); thus their distributions were not normal. Tarantulas have poor vision and cannot see beyond 2.5–5 cm (Baerg 1958); thus their distributions were not normal. Tarantulas have poor vision and cannot see beyond 2.5–5 cm (Baerg 1958); thus their distributions were not normal. Tarantulas have poor vision and cannot see beyond 2.5–5 cm (Baer...
Eastern Michigan University for further observation. Study protocol was approved by the graduate school.

Measuring body condition

Male body condition was monitored over the breeding season by measuring body mass (g) and carapace width (mm) (Jakob et al. 1996). A body condition estimate was made for every male that was newly collected, even if the male was too small (<7.0 g) for a radio transmitter. The carapaces of non-radio-tagged males were marked with small dots of acrylic paint before release so that they could be identified if recaptured. Marking males in this manner is permanent because males do not molt after reaching sexual maturity. The body conditions of males after being radio-tagged were not included in the analyses because of the possible biases introduced through handling, MR measurement, and the provisioning of food and water.

A residual body condition index was used because it has been shown to control for body-size differences better than both the ratio index (body mass/body size) and the slope-adjusted ratio index (based on regression slopes from a reference population) when testing hypotheses about animals from the same population (Jakob et al. 1996). Body condition at the time of first capture (initial body condition) was used to eliminate any bias introduced by providing males with water and a food item after MR measurement. Capture masses (g) were regressed onto carapace widths (mm) and the residuals of ln(x) of body mass used to construct an index. Residuals were then compared with Student’s t tests (Jakob et al. 1996).

Results

Over periods of 58 days during each of the two breeding seasons (2004, 2005), we collected 54 males, 11 females, and 4 subadults on or alongside the roads that intertwine the pastures of the study site. Of these 54 males, 29 were radio-tagged and 26 were tracked for up to 34 days to gather movement, behavior, and MR data (Table 1).

RMR

The RMRs of 30 males (2004: n = 1; 2005: n = 6) were collected over the two breeding seasons. This analysis includes 23 radio-tagged males and 7 individuals (2004: n = 1; 2005: n = 6) that were too small to be fitted with radio transmitters (Table 2). Measurements from five individuals were not included in the analysis because they lacked a low 5 min steady-state period of CO2 production, indicating that they were likely very active and not at rest during the 24 h measurement period. Regression slopes of log10, RMR and log10 body mass for 2004 (n = 12) and 2005 (n = 18) were homogeneous (F(1,27) = 0.93, P = 0.343; Fig. 1). Analysis of covariance was used to test the interaction of year and mass and indicated that RMRs did not differ between the two seasons (F(1,27) = 1.07, P = 0.310). Data from both seasons were pooled because slopes from both regressions were homogeneous.

Simple linear regression was used to compare the relationship between rate of movement and RMR (2004: n = 11; 2005: n = 12). RMR and rate of movement (m/day) were not correlated (R2 = 0.044, P = 0.534) during either year (2004: R2 = 0.067, P = 0.443; 2005: R2 = 0.019, P = 0.662).

Six radio-tagged males were paralyzed by female tarantula hawk wasps (genus Pepsis spp.) during the 2004 season. Only three individuals were able to be removed from the underground brood chambers that they were buried in without injury. Therefore only these three males were used to investigate the effects that wasp venom might have on metabolism. All were paralyzed within 5–7 days of release after the first (baseline) RMR was recorded. The paralyzed RMRs of these individuals were recorded after their extraction from the wasp’s brood chamber. No difference was found between normal and paralyzed mass-dependent RMRs of the three males (paired t = 3.124, P = 0.089).

Daily energy expenditure

The first four measurements of total daily energy expenditure, spanning a period of about 4 weeks of nine radio-tagged males (2004: n = 3; 2005: n = 6) were analyzed using repeated-measures ANOVA to determine if changes in energy expenditure occurred during the breeding season. There was no change between the first four daily energy expenditures of males as the season progressed (F(3,12) = 0.110, P = 0.953).

Circadian periodicity of daily MR

The four period MRs of the first daily MR measurement of 30 males that were captured during both seasons (2004: n = 12; 2005: n = 18) were used in this analysis. Slopes of the regression lines for each of the four periods were homogeneous (F(3,115) = 0.48, P = 0.695). Significant differences did not exist in MR between the four periods (F(3,115) = 2.22, P = 0.090).

Body condition

Body condition indices were constructed (R2 = 0.919, P < 0.000) for 36 males (2004: n = 17; 2005: n = 19). Over the course of both breeding seasons, visual observation of male body condition suggested deterioration over the season. Factors suggesting poor body condition included shrunken abdomens, loss of urticating hairs, and loss of leg movement. We found no difference in the body conditions of males between the two breeding seasons (Student’s t = 0.84, P = 0.407), although more smaller males were found in the second season.

The body conditions of males captured early in the season (late-May to mid-June, n = 22) were compared with the body conditions of males captured later in the season (mid-June to late July, n = 15). No significant differences existed in body condition between early and late captures during both breeding seasons (Student’s t = -0.11, P = 0.912).

Movement

Distances between daily GPS locations were used to determine the approximate overall movement rates of 27 males (2004: n = 12; 2005: n = 15). Males were located every morning (0700–1000 CST) when most had ceased movement and found shelter in a daytime retreat (Stoltey 2007). Mean days radio-tracked differed between the two seasons (2004: 8 ± 5 days; 2005: 12 ± 4 days). There was much variation in rates of movement among males (Table 2, Fig. 2).
Table 1. Data for all radio-tagged male Texas tan tarantulas (*Aphonopelma anax*) for both 2004 and 2005.

<table>
<thead>
<tr>
<th>Tarantula ID. – year</th>
<th>Capture mass (g)</th>
<th>Carapace width (mm)</th>
<th>Total time observed in field (days)</th>
<th>Rate (m/day)</th>
<th>Total distance (m)</th>
<th>Search area (ha)</th>
</tr>
</thead>
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<td>26–2004</td>
<td>9.57</td>
<td>17.9</td>
<td>2</td>
<td>7.28</td>
<td>14.60</td>
<td>0.00</td>
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<td>22–2004</td>
<td>11.20</td>
<td>18.5</td>
<td>1</td>
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<td>49.81</td>
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<td>19–2004</td>
<td>13.42</td>
<td>20.0</td>
<td>2</td>
<td>52.60</td>
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<td>9–2004</td>
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<tr>
<td>25–2004</td>
<td>9.42</td>
<td>17.9</td>
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<td>140.42</td>
<td>280.80</td>
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<td>10</td>
<td>29.23</td>
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<td>17–2004</td>
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<td>3–2004</td>
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<td>7–2004</td>
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<tr>
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<td>17.9</td>
<td>13</td>
<td>258.88</td>
<td>3365.40</td>
<td>29.42</td>
</tr>
</tbody>
</table>

Note: Males are listed in order from least to most distance traveled.

Table 2. Mass (mean ± SE) and metabolic rate (mean ± SE) measured by carbon dioxide production of male Texas tan tarantulas (*Aphonopelma anax*) during both 2004 and 2005.

<table>
<thead>
<tr>
<th></th>
<th>N</th>
<th>Body mass (g)</th>
<th>$V_{CO_2}$ (mL/h) at 30 °C</th>
</tr>
</thead>
<tbody>
<tr>
<td>RMR</td>
<td>30</td>
<td>9.222±0.419</td>
<td>0.338±0.016</td>
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<td>RMR 2004</td>
<td>12</td>
<td>10.309±0.555</td>
<td>0.384±0.021</td>
</tr>
<tr>
<td>RMR 2005</td>
<td>18</td>
<td>8.497±0.538</td>
<td>0.307±0.020</td>
</tr>
<tr>
<td>Daily MR</td>
<td>30</td>
<td>9.100±0.448</td>
<td>0.652±0.038</td>
</tr>
<tr>
<td>Daily MR 2004</td>
<td>12</td>
<td>10.398±0.573</td>
<td>0.655±0.064</td>
</tr>
<tr>
<td>Daily MR 2005</td>
<td>18</td>
<td>8.606±0.542</td>
<td>0.555±0.050</td>
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<td>9.288±0.420</td>
<td>0.509±0.035</td>
</tr>
<tr>
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<td>0.545±0.039</td>
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<tr>
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<td>0.588±0.063</td>
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<tr>
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<td>Period 4</td>
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<td>18</td>
<td>8.549±0.534</td>
<td>0.487±0.047</td>
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Note: Period 1: 0600–1200 CST; period 2: 1200–1800 CST; period 3: 1800–2400 CST; period 4: 0000–0600 CST.
Overall rate of daily movement was significantly higher (141.4 ± 14.2 m/day) during the 2005 breeding season compared with the 2004 breeding season (71.8 ± 12.8 m/day) (Student’s $t = –3.398$, $P = 0.002$). Males frequently moved out of transmitter range between daily observations in 2005, sometimes moving straight-line distances of more than 365 m during the night.

No relationship between male body size and rate of movement was found for the radio-tagged males ($n = 26$) that possessed at least 2 days total time observed in the field (i.e., ≥2 days survival) during either breeding season ($R^2 = 0.094$, $P = 0.114$).

Temperature and humidity were not correlated to distances (m) moved between daily locations for all tracked radio-tagged males ($n = 27$; Fig. 3). These measurements represent the straight-line distance traveled during nightly mate searching activities, which can last for up to 18 h (1636–1053 CST). Daily distances (m) were not related to mean 24 h absolute humidity (gm/m$^3$) in 2004 ($R^2 = 0.008$, $P = 0.33$) or 2005 ($R^2 = 0.001$, $P = 0.625$). Mean 24 h temperature ($^\circ$C) also was not correlated with daily movement (m) in 2004 ($R^2 = 0.034$, $P = 0.044$) or in 2005 ($R^2 = 0.012$, $P = 0.159$). Mean daily absolute humidity (gm/m$^3$) and mean daily temperature ($^\circ$C) at the study site varied both over the season and significantly between the 2 years (humidity: $F_{[1,114]} = 56.79$, $P < 0.001$; temperature: $F_{[1,114]} = 33.26$, $P < 0.001$).

Total linear distances measured between locations also differed between the two breeding seasons. Males moved total straight-line (point-to-point) distances up to 1.7 km in 2004 and up to 3.4 km in 2005. Males that survived the longest moved the greatest distances. Total distances were positively correlated to total time observed in the field ($R^2 = 0.407$, $P = 0.003$) and to rate of movement ($R^2 = 0.574$, $P < 0.001$).

Seventeen males were observed continuously while behavioral and movement data were recorded (2004: $n = 10$; 2005: $n = 7$; Fig. 4). Short survival times, weather (i.e., thunderstorms), or obscuring vegetation prevented all 27 radio-tagged individuals from being observed. Pausing behavior was not caused by an obstacle blocking their path. Males often engaged in a body shake during a pause.
presented with an obstacle (i.e., clump of dense grass), movement continued until it was negotiated and the male was back on the soil substrate. In 2004, the durations for pauses (61 ± 15 s) and walks (160 ± 38 s) of 10 different males during their first 30 min observation were significantly different (Student’s t = 64, P = 0.002). Pause durations (13 ± 2 s) and walk durations (96 ± 11 s) of seven males were also significantly different in 2005 (Student’s t = 28, P < 0.001). Pause durations in 2005 and 2004 were significantly different (Student’s t = 36, P = 0.01). Mean straight-line distances (2004: 9.1 ± 1.2 m; 2005: 13.2 ± 2.7 m) that males traveled between the 5 min marker flags during their first 30 min observation did not differ significantly between the two seasons (Student’s t = –1.56, P = 0.140). Males appeared to move randomly in all directions during these observations, and no correlations between mean daily distance over the season and pause or walk length were found.

Search area

Male search areas were calculated using the minimum convex polygon method. Twenty-six males (2004: n = 14, 2005: n = 12; Fig. 5) having a survivorship long enough to include at least three location data points (GPS) were used in this analysis. Mean search-area size was much smaller in 2004 (1.1 ± 0.5 ha) compared with the search-area size in 2005 (8.8 ± 2.5 ha) (Student’s t = 213, P = 0.002). Radio-tagged males were capable of searching areas up to 29.4 ha, and those with greater total time observed in the field (R² = 0.614, P < 0.001) and higher rates of movement possessed larger search areas (R² = 0.612, P < 0.001). There was a positive correlation between the number of observation points and search-area size for both years (2004: R² = 0.325, P = 0.033; 2005: R² = 0.459, P = 0.022). Search-area size (ha) was not correlated to male body size, measured as carapace width (mm) (R² = 0.049, P = 0.277).

No significant directedness in male movement was seen in either breeding season. Mean days tracked differed slightly between the seasons (2004: 9 ± 2 days; 2005: 12 ± 2 days).

Discussion

RMR and locomotory performance

Results from this study suggest that RMRs in mature male A. anax is not significantly correlated to locomotory performance measured as rate of movement. We predicted that males possessing high maximum MRs, inferred by RMRs (Reinhold 1999; Krasnov et al. 2004; Shillington 2005), would have increased rates of movement and thus cover larger search areas. The variation observed in rate of movement is not sufficiently explained by the small differences in male RMRs. Furthermore, males did not differ significantly in RMRs within or between years. The lack of intraspecific variation in RMR among males suggests that it is a physiological trait that may have been subject to strong selection (Garland et al. 1990) and has acted to stabilize RMR at current levels in this population.

Ultimately, locomotory performance likely sets limits for mate searching behavior in male tarantulas. Locomotory performance in turn is dependent upon underlying traits including RMR, aerobic activity capacity, and respiratory physiology. Although selection is thought to act more strongly on whole-animal traits such as burst speed and endurance, it has been shown that behavior can shelter locomotory capacities from the direct effects of selection, thus increasing their variance and heritability in a population (Garland et al. 1990). This may provide an explanation for the significant differences seen in the rates of male movement. For example, even though males may be able to move at higher speeds, behaviors associated with the reception of female cues or predator avoidance may reduce their overall speed. Therefore the selective importance of male speed may be reduced, and as a result both the variance and heritability of male movement rates would be increased in the population (Garland et al. 1990; Garland and Losos 1994).

Although male mobility has been shown to have significance in scramble–competition–polygynies, other phenotypic
correlates relating to mating success such as perceptiveness (Alcock 1979) and spatial memory (Gaulin and FitzGerald 1986) may also be important (Schwagmeyer 1988). In addition, it is possible that male traits conferring endurance are more important than locomotory ability in extreme environmental conditions or marginal populations (Purse and Thompson 2005), and that selection for other traits (Plaistow and Siva-Jothy 1996) which confer endurance ability in these conditions is favored. Selection may also act strongly on traits conferring predator avoidance or deterrence and may be even more important than locomotory ability or endurance. Animals in this study were affected by predation during both years (Stoltey 2007), and missing patches of urticating hairs indicating male defensive behavior were common in individuals captured throughout both seasons. In light of these findings, additional studies are needed to investigate other phenotypic components or traits that may be important to male mating success.

**Daily energy expenditure**

The daily energy expenditures of radio-tagged males did not change over the course of the season. The MRs of an individual that died inside the metabolic chamber after having survived for 5 weeks did not decline until just a few hours before death. Perhaps the increased energetic demands associated with mate searching prevent males from depleting their metabolism to conserve energy when exposed to conditions of low prey availability or starvation (Anderson 1974; Humphreys 1977). More likely, the short life expectancy of male tarantulas, in general, reduces any longer term benefit derived from energy conservation. By not depressing MRs, mature males would always be energetically prepared to search for mates, engage in courtship, and defend against or escape from predators. Thus selection might favor males having high rates of activity instead of those individuals that conserved energy and were less active. As a result, mating success would be increased by maximizing short-term survival and not the speed of mate searching.

**Initial body condition**

The initial body condition of males measured early in the breeding season (late May to mid-June) did not differ from those collected late in the season (late June to mid-July). This is an interesting result, as both initially captured males and radio-tagged males appear to be in poor physical condition later in the season (Janowski-Bell and Horner 1999; Shillington 2002; C. Shillington, personal observation). Emaciated abdomens indicating depleted energy reserves and other visual declines in male body condition characterized by lethargy and loss of leg movement, observed over the course of the breeding season, were not unique to this study and have been previously reported in *A. anax* (Shillington 2002), as well as two other North American tarantula species (Prentice 1992; Janowski-Bell and Horner 1999) and two South American tarantula species (Pérez-Miles et al. 2005).

As a spider depletes its abdominal food stores, the corresponding decrease in body volume negatively affects locomotory abilities (Anderson 1974). Starving wolf spiders (*Lycosidae*) ingest water frequently, and severely starved individuals with shrunken abdomens lose the ability to move (Anderson 1974). Locomotory abilities can be restored in these individuals after enough water is ingested to replace lost abdominal volume (Anderson 1974).

Males were, on occasion, observed either feeding or in the process of capturing prey (i.e., genus *Scolopendra* L., 1758; Phasmatodea). Prey capture by males has been previously reported in *A. anax* (Shillington 2002) and in Texas brown tarantulas (*Aphonopelma hentzi* (Girard, 1852)) (Punzo and Henderson 1999). Although the habitat was extremely dry for extended periods, males were observed drinking condensation that formed on vegetation (T. Stoltey, personal observation). Wandering males may regularly have access to both food and water, but it is not known how often they feed and drink to maintain their energy reserves. In general, most male spiders are not known to catch prey or feed after they become sexually mature (Foelix 1996). It is possible that emergence from burrows at the start of the season could be staggered and newly emerged individuals with good body condition were collected throughout the season.

**Search-area size and movement**

Males were capable of searching large areas of habitat, up to 29 ha at speeds of 365 m/day, during the breeding season. The highest rate of movement previously reported for a mature male *A. hentzi* during the breeding season was 94.9 m/day (Janowski-Bell and Horner 1999). We observed 16 male *A. anax* with movement rates >90 m/day (90.7–258.9 m/day). In addition, this study provides the first known estimation of search-area size for a male theraphosid, and unlike similarly sized vertebrate ectotherms, body sizes were not positively correlated to the search-area size (Christian and Waldschmidt 1984). Instead, males with greater total time observed in the field (i.e., survived the longest; Stoltey 2007) and highest rates of movement possessed the largest search areas.

Male activity was characterized by periods of continuous movement, which were interrupted by brief periods of inactivity or pausing. Mean pause length was longer than a single cycle of limb movement, and therefore male movement could be characterized as intermittent (Kramer and McLaughlin 2001). This type of locomotion has been described for many other species including other spiders (Kraft and Pasquet 1991; Jackson and van Olphen 1992; Weinstein and Full 1992). Males spent more time walking and less time pausing during 30 min observations during both years. Pause durations were significantly longer in 2004, although there were no significant differences in walk durations or distances traveled during the 30 min observations. From a metabolic cost perspective, longer pause durations require more time spent at an elevated metabolic state with no increase in travel distance, and as a result, animals can minimize costs by moving faster for a longer duration (Baker and Gleeson 1999; Hancock and Gleeson 2005). In contrast, endurance or distance capacity increases with longer pause periods as a response to partial recovery processes, which allow the activity to be repeated more frequently (Hancock and Gleeson 2005).

In conclusion, RMR was not significantly correlated to rate of movement, body size, or search-area size, although increased activity capacity is typically associated with increased RMR as explained by the aerobic capacity hypothe-
sis. Instead, those individuals that survived the longest were able to search the largest areas. It appears that males are using intermittent locomotory behavior but are not necessarily increasing their locomotory endurance. The lack of change in the body condition of newly captured males as the season progressed suggests that even though there appears to be a mass emergence of males at the beginning of the season in late May, “new” males continue to emerge over the first half of the season. It is not known when or how long individuals spend in the burrow after becoming sexually mature. A better method would be to monitor the body condition of a group of radio-tagged males that remained in the field during the course of the season without being held in the laboratory for short periods of time. Daily energy expenditures did not decline over the course of the season and may indicate that factors associated with mate searching are more important than energy conservation.

Few females or their burrows were discovered during this study and future studies would benefit from data describing the location and densities of females. Our data show that males are able to search large areas, and therefore, habitat type and fragmentation likely affect male movement and thus the frequency of male–female encounters.

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