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MOVEMENT OF THE MALE BROWN TARANTULA, *APHONOPELMA HENTZI* (ARANEAE, THERAPHOSIDAE), USING RADIO TELEMETRY

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ABSTRACT. This study was designed to gain insight into the ''migratory'' life history component of the male brown tarantula, *Aphonopelma hentzi* (Girard 1854), and to determine if radio telemetry could successfully answer questions regarding the ecology of theraphosids. Tarantulas were equipped with radio transmitters and movement monitored using an antenna and radio receiver. Overall movement of males was in all directions and randomness could not be excluded as a factor. Individual males moved relatively large distances, up to 1300 m, and significant directedness was only found in three individuals. In addition, notes on habitat, ecology and behavior are presented.

Many spiders disperse over large distances by ballooning, and this is well documented in the aranemorphs (Weyman 1993, 1995; Weyman et al. 1995). Mygalomorph spiderlings have been observed ballooning over short distances (Bristowe 1939; Coyle 1983, 1985; Coyle et al. 1985); and Coyle (1983, 1985) concluded that ctenizid spiderlings could travel significant distances if they launch from taller vegetation. However, immature tarantulas (Theraphosidae) are not known to balloon. There is no mention in the literature of the large scale movement of male tarantulas. This study was designed to determine the large scale distance and direction traveled by the mature male tarantula, *Aphonopelma hentzi* (Girard 1854), using radio telemetry.

Mature males leave their burrows to search for mates from June to December (Baerg 1928, 1958; Gertsch 1979; Minch 1979a). Individual males have been observed crossing highways, appear to be moving in the same direction, and resist being redirected (Baerg 1958, 1963). Baerg (1958) stated that rarely are the movements of hundreds of individuals reported. Magnusson (1985) witnessed a coordinated movement of 89 male *Cyclosternum* sp. in Brazil. Mass movements could occur when weather conditions are ideal for travel (Baerg 1958). In addition, Baerg (1958) proposed a general ''migration'' of tarantulas throughout the southwestern United States, Mexico, and possibly Panama. Baerg (1958) also suggested that reduced inbreeding could result from males moving large distances in search of mates.

Migration differs from dispersal in many respects. Dispersal typically refers to the movement of individuals in a population that results in an increase in the mean distance between individuals (Andrewartha & Birch 1954; Southwood 1981; Dingle 1996). According to Danthanarayana (1986) and Dingle (1996), migrants usually exhibit five basic behavioral characteristics: 1) persistent movement, 2) undistracted by the presence of resources promoting growth and maintenance (Kennedy 1961), 3) ''straightened out'' movement, 4) distinct leaving (Southwood 1962) and arriving behaviors, 5) reallocation of energy specifically to support movement.

In the United States *Aphonopelma* can be found west of the Mississippi River to the Pacific Coast and north into Arkansas, Utah, and Nevada (Baerg 1928; Gertsch 1979; Roth 1993). They are typically found on hillsides covered in sparse vegetation and mixed with diverse desert growth (Baerg 1928, 1958; Gertsch 1979). Tarantulas are usually nocturnal, but may be active from late afternoon into late morning when light levels are low (Baerg 1958; Comstock 1975; Minch 1978).

Radio telemetry is an effective tool for collecting data on organisms that are difficult to follow, observe or relocate (Mech 1983). His-

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torically, it has been used extensively to follow the movements of larger animals (Mech 1983). As technology decreased the size of transmitters, this technique has been increasingly applied to smaller invertebrates including crayfish (Covich 1977), crabs (Gherardi et al. 1987, 1988a, b, c; Gherardi & Vannini 1989; Fletcher et al. 1990), snails (Bailey 1989; Tomiyama & Nakane 1993), and insects (Hayashi & Nakane 1988, 1989; Riecken & Raths 1996). Radio telemetry may provide unique insights into the ecology and behavior of the larger arachnids. This technology is used to study the brown tarantula, *A. hentzi*, an ideal subject for radio telemetry due to its activity, abundance and size.

METHODS

Study site.—The study was conducted on the W.T. Waggoner Estate, 19.4 km WSW of Electra, Wilbarger County, Texas (33°58′N, 99°08′W). This area is part of the Rolling Plains region of Texas, which is a subsection of the Great Plains region of the central United States (Lewis 1962). It is characterized by rolling-to-rough topography broken by intermittent streams (Lewis 1962). Annual rainfall for the area is approximately 76.2 cm, with May and September being the wettest months (Lewis 1962). The dominant vegetation is scrub mesquite (*Prosopis*), goat bush (*Castela*), prickly pear cactus (*Opuntia*), turkey cactus (*Opuntia*), little blue stem (*Schizachyrium*), mesquite grass (*Bouteloua*), and broom weed (*Xauthocephalum*). The southern portion of the study site is dissected by a paved farm-to-market road running east to west. The area is broken by occasional dirt or gravel maintenance roads. Past and current land use at the site include oil production and cattle grazing.

Transmitters and receiver.—All radio telemetry equipment was purchased from Wildlife Materials, Inc. (Carbondale, Illinois). A model TRX-1000S receiver was used with a folding three-element yagi directional antenna. The frequency range used was 150.000–150.999 Mhz. Each transmitter (SOPB-2011) had a different frequency thereby identifying individuals. Transmitters weighed approximately 0.6–0.8 g and were 9 × 5 × 4 mm. The flexible antenna, constructed of wire similar to guitar string, was 7.62 cm in length. To prevent possible chafing of the abdomen and to provide minimal physical contact the antenna was bent upward at a 45° angle.

Procedure.—Male tarantulas were equipped with transmitters from 2 September–17 October 1994 and from 9–19 July 1995. They were captured in a clear plastic container on predominantly open ground. Individuals were examined to determine overall physical condition. Those lacking obvious physical abnormalities and exhibiting activity were weighed (to the nearest 0.1 g) using an Ohaus LS200 portable scale. The only exception was specimen #13-94, which was missing the third left leg. Males ranged from 2.5–7.5 g. They were anesthetized with carbon dioxide for 2 min or until docile. Tarantulas were then placed on a thick synthetic sponge with legs extended. Their legs were restrained by placing a second sponge which had been cut to expose the cephalothorax and abdomen over the first sponge. String was used to hold the two sponge pieces in place. This restrained the spider and facilitated attachment of the transmitter. To assist in the attachment of the contact adhesive, the ‘‘hairs’’ (setae) were removed from an area on the carapace, posterior to the eyes, by gently rubbing the area with a pair of forceps. A small amount of waterproof contact adhesive was placed on the the carapace and on the transmitter. After 5 min the adhesive on the transmitter was pressed into the adhesive on the spider. This was allowed to set for 20–40 min before the tarantula was removed from the sponge and placed back into the capture container. Equipped tarantulas (Fig. 1) were released at the exact site where they were collected within 2 h of capture.

Tarantulas monitored in the fall of 1994 were observed a minimum of three days per week, while those in 1995 were observed once everyday, weather permitting. Locations of spiders were marked and labeled using flagging tape on adjacent vegetation. Direction traveled since the last observation was determined by compass. Readings were corrected to reflect true north. Approximate distance traveled between observations was obtained using a tape measure or by pacing.

Seventeen *Aphonopelma hentzi* males were monitored in the Fall of 1994 for movement. Of these, seven individuals retained their transmitters for four or more days and were considered for data analysis. This yielded a total of 113 observations. Six additional males

Figure 1.—*Aphonopelma hentzi* male with attached radio transmitter.

were monitored in July 1995. These individuals were checked for short-term movement once every 24 hours. Four of these individuals retained their transmitters for three or more days, and yielded 20 observations.

Identification.—The tarantula population studied was identified as *Aphonopelma hentzi*. Representative specimens are on deposit in the American Museum of Natural History, New York. The study site lies outside the known distribution reported by Smith (1994) for three species in the region. As a result, a name could not be assigned to this spider using Smith's (1994) descriptions. The validity of Smith's species are in question (Prentice 1997). Cokendolpher (pers. comm.) noted that Smith failed to take individual variation into account. Therefore, the old name is applied to the common tarantula of Texas and Oklahoma. Representative specimens from the area were confirmed as *A. hentzi* by Dr. Rick West, Research Associate, Royal B.C. Museum (West pers. comm.).

Statistics.—The samples from each year were compared using the Mann Whitney *U*-test for unmatched pairs (Fowler & Cohen 1990). There was a difference between the samples when weight was considered ($U = 0$, $P < 0.05$). However, there was no difference between the samples when the rate ($U = 10$, $P > 0.05$) and inflection points per day ($U = 14$, $P > 0.05$) were considered. Based upon these data, the samples from both years were combined for statistical analysis except where indicated.

RESULTS

Movement.—Figures 2–6 illustrate the movement of males and give a brief description of the habitat for each observation. The weight ($\bar{x} = 5.0 \pm 1.5$ g SE), total time observed, total path distance, rate ($\bar{x} = 53.8 \pm 25.7$ m/d SD), number of inflection (turning) points per day ($\bar{x} = 0.64 \pm 0.19$ SD), point-to-point distance (distance from the first observation to the last observation), and point-to-point angles with 0° being north (angle from first observation to last observation) ($\bar{\phi} = 253.6° \pm 70.8°$ SD) for each male are presented in Table 1. Male #12-94 traveled the farthest with regard to both point-to-point distance and rate (Fig. 4, Table 1). The most inflection points per day was exhibited by #5-94 in 1994 (Fig. 6, Table 1) and #1-95 in 1995

Table 1.—Individual tarantula number, weight, days observed, total distance of path traveled, rate of travel per day, number of inflection points per day, distance from first observation to last observation, direction from first observation to last observation.

Spider #	Weight (g)	Total time observed (d:h:min)	Total path distance (m)	Rate (m/d)	Inflection points per day	Point-to-point distance (m)	Point-to-point angle (degrees)
1-94	—	4:18:35	148.8	31.2	0.60	102.1	236
5-94	7.0	24:00:00	1320.2	55.0	1.00	677.3	327
9-94	6.6	4:17:26	281.4	59.6	0.60	208.2	141
10-94	6.2	7:17:14	412.8	53.5	0.75	264.2	114
12-94	7.5	18:10:27	1750.2	94.9	0.72	1360.4	305
13-94	5.3	4:15:48	123.9	26.7	0.60	116.9	228
18-94	6.6	13:22:26	364.2	26.1	0.50	272.2	313
1-95	3.6	9:22:09	815.6	82.2	0.80	324.6	98
2-95	—	3:00:34	211.1	69.9	0.66	188.3	215
3-95	2.6	2:22:50	222.2	75.8	0.66	176.3	243
6-95	4.2	3:22:55	69.2	17.7	0.25	14.1	6

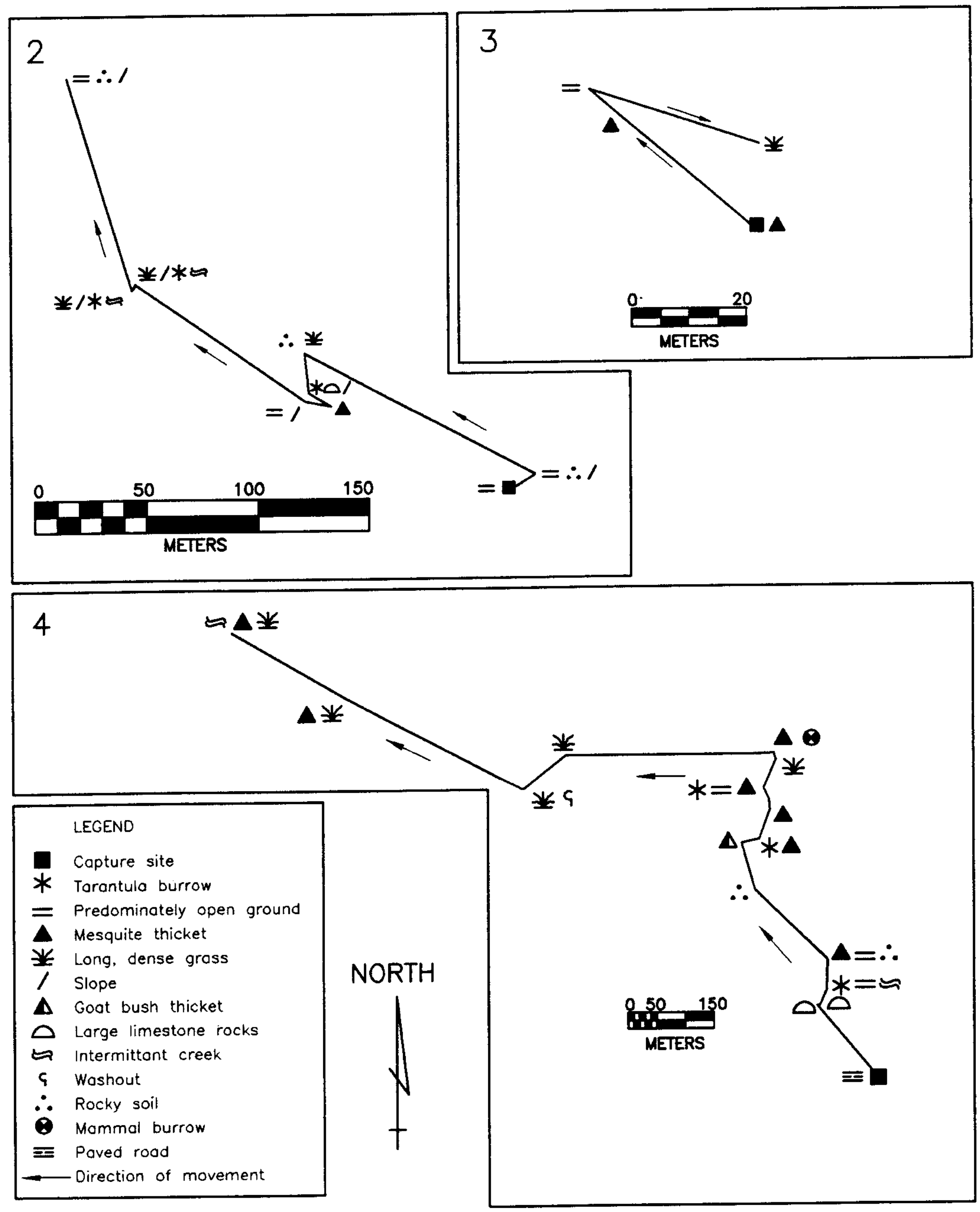
(Fig. 5, Table 1). Male #6-95 traveled the least with respect to rate, inflection points per day and point-to-point distance (Fig. 3, Table 1). There was no correlation between tarantula weight and rate ($r_s = 0.10$, $n = 9$, $P > 0.05$). However, there was a marginally significant correlation between rate and inflection points per day ($r_s = 0.68$, $n = 11$, $0.02 < P < 0.05$).

Overall movement of individual males was in almost all directions (Table 1). The Rayleigh test [uses the mean vector (r) to determine directedness (Batschelet 1981)] could not exclude randomness as a factor in the point-to-point movement of the combined samples from both years ($r = 0.23$, $n = 11$, $P = 0.5$) or of the sample from 1994 ($r = 0.31$, $n = 7$, $P = 0.55$). However, the movement of male #5-94 ($r = 0.46$, $n = 26$, $0.001 < P < 0.004$; $\bar{\phi} = 328.9° \pm 59.7°$ SD) and male #12-94 ($r = 0.62$, $n = 18$, $P < 0.001$; $\bar{\phi} = 335.4° \pm 49.7°$ SD) indicated directedness. The results from Rao's spacing test [uses angular data to determine directedness (Batschelet 1981)] yielded similar results with one exception; #13-94 exhibited directedness ($U = 188$, $n = 5$, $P < 0.05$; $\bar{\phi} = 247.1° \pm 34.1°$).

Performance of transmitters.—All transmitters, except one, were recovered in working order at the end of the study. The transmitter attached to #5-94 was recovered completely wrapped in silk within the entrance of a tarantula burrow. There were abrasions and breaches on the epoxy coating of the transmitter and a very large tarantula with a taunt abdomen was observed within the burrow. There was no correlation between rate (m/d) and the percentage of the transmitter weight to body weight ($r_s = 0.104$, $n = 9$, $P > 0.05$). Three transmitters were known to have been removed from spiders within burrows. These transmitters were tightly wrapped in silk, and recovered just inside the burrow or a few centimeters from the burrow entrance.

Microhabitat and refugia.—Males were found moving through a variety of habitats from relatively barren, rocky ground to areas of dense vegetation. Tarantulas were observed to be traveling easily through the grass many centimeters above the ground. One male was observed hanging from vegetation several centimeters above the ground.

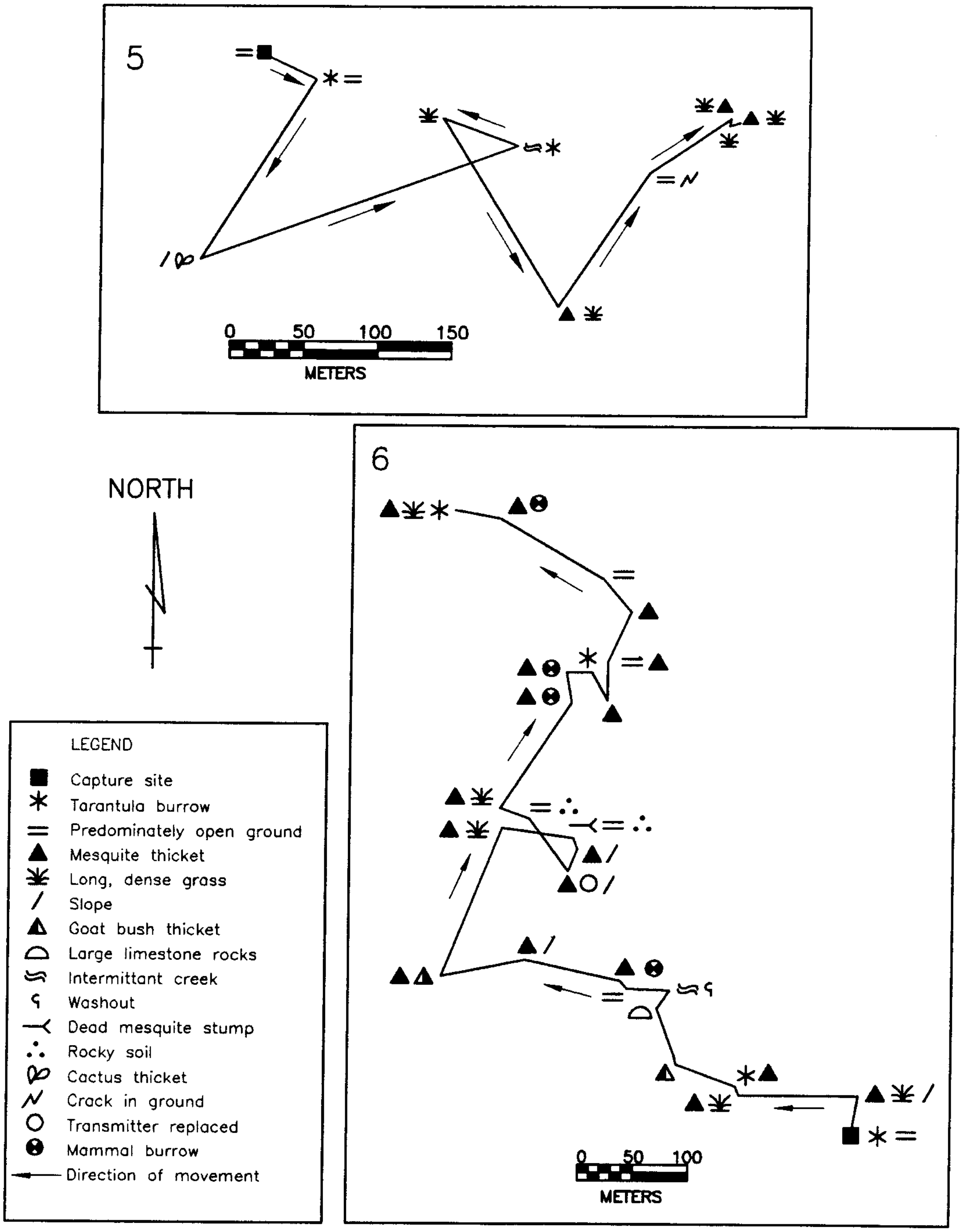
Most males were inactive during the day and remained in sheltered environments (e.g., scrub thickets). Scrub thickets were 1–3 m in height, 1–3 m in diameter and dominated by mesquite (*Prosopis*). Other plants included goat bush (*Castela*), prickly pear cacti (*Opuntia*), turkey cacti (*Opuntia*) and an understory of dense grasses (*Schizachyrium*, *Bouteloua*). Several small mammal burrows, outcroppings, and large limestone rocks were also used for shelter during the day. One locale, characterized by limestone slabs 0.5 m in diameter and interspersed in dense grass, attracted three males within two days yielding a total of five observations. The abundance of data obtained



Figures 2–4.—Movement of *Aphonopelma hentzi* males. 2. Male #18-94 had the lowest rate and number of inflection points per day in 1994; 3. Male #6-95 had the lowest rate and number of inflection points per day in 1995; 4. Male #12-94 had the highest rate in 1994.

at this locale was not typical of data collected during the rest of this study.

Seven males were found within burrows with individuals that were assumed to be mature females. Males remained at these locales from 1–3 days before continuing movement. Female burrows were found by males within thickets, in dense grass and on open ground.



Figures 5, 6.—Movement of *Aphonopelma hentzi* males. 5. Male #1-95 had the highest rate and number of inflection points in 1995; 6. Male #5-95 had the highest number of inflection points per day in 1994.

Males probably visited more female burrows than detected due to the cover provided by dense vegetation. These ''locales'' or ''sites'' were not closely inspected for fear of disturbing the males and biasing movement results.

Behavioral observations.—On 2 September 1994 male #1-94 was observed mating with a female approximately 0.5 m from the entrance of the female's burrow on barren soil. Upon approach the spiders separated and then the female quickly retreated into her burrow. The male was captured and outfitted with a transmitter. Male #5-94 was 45.7 cm from her burrow for at least 18:54 h.

On two separate occasions males were observed moving in overlapping counter-clockwise circles 60–90 cm in diameter. This is similar to observations made by Shillington & Verrel (1997).

Observations towards the end of the summer indicated most males continually lost body mass and ultimately possessed very small abdomens. On the morning of 3 October 1994 male #12-94 (Fig. 4) was found in the open, positioned vertically with his abdomen in the air. The last two pairs of legs were stroking the antenna of the transmitter. His abdomen was very small. In the evening he was found dead, legs curled under the shrunken abdomen. Males #2-95 and #3-95 were also found dead. However, males #1-95 (Fig. 5) and 6-95 (Fig. 3) were recovered, transmitter removed, and released at the end of the 1995 study period.

DISCUSSION

The movement of male tarantulas has been a subject of speculation and interest to arachnologists for many years (Smith 1994). Most of what is known regarding the ecology of male tarantulas has been obtained from studies regarding the ecology of female and immature individuals within the proximity of their burrows (Minch 1978, 1979a, b, c; Kotzman 1990; Shillington & Verrell 1997) or in the laboratory (Baerg 1938, 1963), with two known exceptions (Baerg 1958; Sanderson 1988 as cited by Smith 1994). This is the first study known to extensively document the movement of male tarantulas.

Radio telemetry proved to be useful and enabled us to obtain data that would have been difficult to acquire using other methods. The performance of the transmitters was excellent. The signal could be detected several hundred meters from the spider. In addition, the males could be located easily when in burrows and under rocks. It was assumed the transmitters would have a minimal effect upon the movement of individual tarantulas. Maneuverability in small spaces was a concern, but the antenna proved flexible enough to allow males to enter and remain in burrows. Tagged males were observed crawling around or past residing females within the burrow.

Attachment of the transmitter to the tarantula was a problem. Many of the contact adhesives used did not maintain their bond. This resulted in several spiders losing their transmitters within a few days and was the limiting factor of this study.

Organisms use a hierarchical set of cues to locate resources and exhibit behaviors appropriate for each level: habitat, patch, individual resource. (Bell 1991). It has been shown (Baerg 1958; Minch 1979c; Shillington & Verrel 1997) that male tarantulas are able to detect local ''cues'' provided by females in the vicinity of their burrows. These have not been shown to be directional, but do elicit local search behavior described as ''animated circular motion'' (Shillington & Verrel 1997), and were observed in this study. Baerg (1928, 1958), Gabel (1972), and Kotzman (1990) have noted the clumped or patchy distribution of theraphosid burrows. Theraphosids are almost blind and cannot see beyond 2.5–5 cm (Baerg 1958). As a result, it is unlikely tarantulas use visual environmental cues when searching for burrow patches. Bell (1991) proposed several search strategies organisms may adopt when lacking environmental cues while searching for resource patches: random walk, straight line, systematic movement pattern (spiral or parallel movement), kinesthetic-input mapping or a combination of these strategies. The results of this study did not reveal a systematic movement pattern, and this may be because observations were not at the appropriate scale. Three large scale loops were observed among individuals considered for data analysis (Figs. 5, 6). These imply male tarantulas are conducting systematic searches to locate mates within ''colonies.'' The movement of searching males between ''colonies'' may be a combination of random walks and straight line movements as indicated by the directedness expressed in only a few individuals. However, the lack of directedness may be a function of the time individuals were followed.

There was limited evidence to support the axiom that male tarantulas are migrating using Dingle (1996) and Danthanarayana's (1986) definition. Based upon their observations of North American tarantulas, Baerg (1963) and Minch (1978) report that males travel farther during the mating period than any other period of the life cycle. There was some evidence that movement of individuals was directed. Later in the season males were observed with notably smaller abdomens indicating energy may be reallocated specifically for movement. Male #12-94 (Fig. 4) moved 30% (537 m) of the total distance (1750 m) in 9% (1 day, 16h, 25 min) of the total time (18 days, 10h, 27 min). Baerg (1928) and Minch (1979c) noted that males die at the end of the mating season. Their observations noted that preceding death the abdomen becomes shrunken, ability to extend legs is lost, and overall sluggish behavior occurs. There was little evidence for a synchronized, directional movement of all males sampled. As a result, no definitive conclusions can be drawn regarding the characterization of the movement of male tarantulas as migratory. Further behavioral studies would serve to elucidate the characterization of this behavior.

Early summer males were smaller in size and weight. As a group they were not significantly different with respect to their rate and inflection points per day, and they behaved the same ecologically with regard to movement. Further study is needed to determine if the early males have overwintered as adults or simply molted earlier than the late summer brood.

Males frequented scrub thickets, small mammal burrows and large limestone rocks throughout the study. These habitats probably provided protection from predators and allowed better thermoregulation during the day. In addition, the locale characterized by limestone rocks may have a high density of mature females not observed due to burrows being hidden by the rocks.

Males were frequently found within tarantula burrows in the presence of other individuals. These were presumed to be mature females and males were courting and mating with them. Multiple matings with the same female are probable given the length of time males were in the presence of these females, which ranged from one to several days. Males also visited multiple females (Figs. 2, 4, 5, 6). The data reflect fewer matings than probably occurred due to sampling and lack of detection within thickets. Baerg (1958) suspected mating occurs primarily inside the burrow. However, male #1-94 was observed mating with a female approximately 0.5 m from her burrow entrance.

This study indicates radio telemetry is a valuable technique for studying the movement of male *Aphonopelma hentzi*. Males were observed moving large distances, up to 1300 m, over a significant period of time, up to 18 days, while searching for mates. Current research on the behavior and ecology of movement in tarantulas includes: evaluation of extensive movement, influence of different habitat types, effect of habitat fragmentation.

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