

Microhabitat utilisation, diet composition, intraguild predation, and diel periodicity in five sympatric species of desert arachnids: a wolf spider (*Hogna carolinensis*), tarantula spider (*Aphonopelma steindachneri*), solifuge (*Eremobates palpisetulosus*), giant whipscorpion (*Mastigoproctus giganteus*), and scorpion (*Diplocentrus bigbendensis*)

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Summary

This study investigated microhabitat utilisation (soil and vegetation type), diet composition, intraguild predation, and diel periodicity in five sympatric species of arachnids at Persimmon Gap in Big Bend National Park (BBNP): a tarantula (*Aphonopelma steindachneri*), wolf spider (*Hogna carolinensis*), solifuge (*Eremobates palpisetulosus*), giant whipscorpion (*Mastigoproctus giganteus*), and scorpion (*Diplocentrus bigbendensis*). A total of 1389 arachnids were collected during early spring to later summer 2002. For all species, females were larger than males. There were non-random associations of all species of arachnids across soil types. Over 41% of all arachnid species were found on sand loam soils (soil hardness: 7–8.9 kg cm⁻²), followed by 25.3% on clay loam (9–11 kg cm⁻²), 17.8% on silt loam (3.5–6.5 kg cm⁻²), 9.9% on adobe (36–39 kg cm⁻²), and 5.6% on sand (0.6–2.2 kg cm⁻²). A significantly greater proportion of whipscorpions and scorpions were found on harder adobe soils as compared with the spiders and solifuges. A total of 663 arachnids (47.8%) were found in areas dominated by mixed scrub. No differences in diet were found between sexes for any arachnid species. Prey items found in the chelicerae indicate that these animals are generalist predators and feed on a variety of ground-dwelling arthropods. Beetles comprised between 11 and 31% of the prey items, followed by orthopterans (7–23%), caterpillars (Lepidoptera, 1–30%), hemipterans (2–7%), and cockroaches (0–6%). For arachnid prey, values were: spiders (7–18%), scorpions (4–8%), and solifuges (6–15%), showing intraguild predation among these arachnids. Values for Levins' measurement of trophic niche breadth were: 0.4583 (*A. steindachneri*), 0.4424 (*H. carolinensis*), 0.4288 (*E. palpisetulosus*), 0.4508 (*M. giganteus*), and 0.3887 (*D. bigbendensis*). All arachnid species showed pronounced nocturnal activity patterns. Levins' indices for temporal niche breadth were: 0.5821 (*A. steindachneri*), 0.5521 (*H. carolinensis*), 0.4983 (*E. palpisetulosus*), 0.4637 (*M. giganteus*), and 0.5057 (*D. bigbendensis*). The results indicate that soil hardness is an important factor in determining the distribution of these arachnids, and that they are potential competitors for food and shelter sites at Persimmon Gap in BBNP, and take part in intraguild predation.

Introduction

A major topic of interest in ecology is the analysis of species assemblages (guilds) that use their environment in similar ways. Guild structure is often associated with several factors (Polis, 1990; Moran & Hurd, 1997). One involves interference competition (agonistic interactions, territoriality) which can result in selection that favours behaviour that causes subordinate individuals to avoid dominant ones. A second factor involves exploitation competition for limited resources such as food, space, or

shelter sites, which selects for ecological divergence of species with respect to resource utilisation. This type of divergence reduces niche overlap and increases the opportunity for coexistence. Other factors such as severe physical disturbance (storms, fire, drought, volcanic activity, etc.) and predation may act to restrict the distribution or abundance of particular species to a greater or lesser extent than other species that may be better adapted.

In Big Bend National Park (BBNP), which lies in the northern region of the Chihuahuan Desert, five sympatric species of large, ground-dwelling arachnids can be found, which are major faunal components of an insectivore guild (Punzo, 2000a). Although there are other species of wolf spiders, solifuges, and scorpions that occur in BBNP, the adults of all these five species, which were chosen for this study, can attain body lengths >4.5 cm. These arachnids are the giant whipscorpion *Mastigoproctus giganteus* (Lucas) (Uropygi), scorpion *Diplocentrus bigbendensis* Stahnke (Scorpiones: Diplocentridae), tarantula spider *Aphonopelma steindachneri* (Ausserer) (Araneae; Theraphosidae), wolf spider *Hogna carolinensis* (Walckenaer) (Araneae: Lycosidae), and solifuge *Eremobates palpisetulosus* Fichter (Solifugae: Eremobatidae). All of these arachnids are primarily nocturnal during late spring and summer months, and typically feed on a variety of ground-dwelling arthropods, as well as small lizards and snakes (Punzo, 1998a, 2000a; Punzo & Ludwig, 2006). Also, large theraphosid spiders are known to feed on small rodents and/or their neonatal young (Baerg, 1958; Marshall, 1989).

In addition to some species of arachnids feeding on similar prey items, they may also feed on one another, a phenomenon known as intraguild predation (Polis *et al.*, 1989). For example, although no data are available on the diet of *D. bigbendensis*, other species of desert scorpions are known to cannibalise one another, as well as prey on other species of scorpions and spiders (Polis & McCormick, 1987). The tarantula *Aphonopelma chalcodes* Chamberlin, from the Sonoran Desert, is known to feed on smaller conspecifics as well as on other spiders (Minch, 1977). Solifuges from the Sonoran and Chihuahuan Deserts are known to feed on conspecifics as well as on spiders and scorpions (Punzo, 1998a, b). However, the extent to which *A. steindachneri*, *H. carolinensis*, *E. palpisetulosus*, *M. giganteus* and *D. bigbendensis* prey on one another is not known.

Not only is there the potential for interspecific competition for food, but also for shelter and nesting sites. Females of *A. steindachneri* construct burrows where they remain for extended periods of time (Breene *et al.*, 1996). Males are not strongly fossorial and usually seek refuge under rocks or surface plant debris and within rock crevices (Smith, 1994). Smaller juveniles of *D. bigbendensis* seek refuge under rocks and within rock crevices, whereas larger individuals burrow into the ground (Warburg & Polis, 1990). *Eremobates marathoni* Muma and *M. giganteus* also seek shelter under rocks and in crevices (Punzo, 1998b, 2001). In some areas of the Chihuahuan Desert, adults of *H. carolinensis* are

known to either construct burrows or use shallow depressions under rocks as shelter or nesting sites (Punzo, 2003). Additionally, the quality of nesting sites is important because female tarantulas remain in their burrow with their egg sac (Punzo & Henderson, 1999), while wandering wolf spider females carry their egg sacs with them attached to their spinnerets (Stratton, 1985). When occupying a burrow, *H. carolinensis* females often carry the egg sac to the burrow entrance to expose it to warm air temperatures during certain times of the day, and aggressively defend their sacs against potential predators (Shook, 1978).

The purpose of this study was to test the hypothesis that *A. steindachneri*, *H. carolinensis*, *E. palpisetosus*, *M. giganteus* and *D. bigbendensis* are competitors for food, space, and shelter sites in the northern Chihuahuan Desert, and to assess the degree of intraguild predation that may occur.

Description of the study area

This project was conducted during 2003 at Persimmon Gap (PG) which is located on the northern boundary of Big Bend National Park (BBNP; Brewster County), in Trans Pecos Texas. This region of Texas lies within the northern region of the Chihuahuan Desert. The study site (20°37'N, 103°04'W) was a circular plot around the northern entrance to the Park, with a radius of 1.2 km. The climate at this site is arid, and the annual rainfall at PG during 2003 was 17.6 cm, with 80% of rainfall occurring from May through September. Daily mean air temperatures ranged from 7–15.5°C in January and February, to 26.7–43.4°C during July and August (U.S. Dept. Interior, 2003).

There is a wide range of topographic diversity within BBNP. Persimmon Gap (PG) lies on a desert floodplain with internally-draining basins, limestone deposits, alluvial fans, gypsum flats, salt playas, and freshwater seeps and springs (Maxwell *et al.*, 1967), with some areas containing dense to scattered clumps of vegetation, while others have little or no vegetation (Punzo, 2003). PG is characterised by a desert scrub habitat, with some areas of ground containing rocks or gravel, while others are devoid of vegetation and rocks. Dominant vegetation at the study site included vegetation types (zones) dominated either by mesquite (*Prosopis glandulosa*), creosote bush (*Larrea divaricata*), sotol (*Dasyliiron leiophyllum*), lechuguilla (*Agave lechuguilla*), mixed scrub (tar brush *Flourensia cernua*, prickly pear cactus *Opuntia engelmannii*, ocotillo *Fouquieria splendens*, catclaw *Acacia greggii*, thistle *Cirsium turneri*, and scattered clumps of grasses including fluff grass *Erioneuron pulchellum* and chino gramma *Bouteloua breviseta*), and areas devoid of vegetation (barren). Some areas of the study site have a variety of decaying plant debris on the ground surface which, along with depressions under rocks, rock crevices, and rodent burrows, can provide shelter sites for arthropods. A detailed description of the vegetative zones of BBNP can be found in Hendrickson & Johnston (1986).

Persimmon Gap has a variety of soils. I have used the terminology of Gonzalez-Cortes (1959) to describe various types of soils found in the Chihuahuan Desert. At PG, major soil types (with their soil hardness values) include adobe (36–39 kg cm⁻²), clay loam (9–11), sand loam (7–8.9), silt loam (3.5–6.5) and sand (0.6–2.2).

Methods

Collection of animals, morphometric measurements, and field studies

Collection and/or observation of specimens occurred between 10 April and 5 September 2003. Previous studies have shown that these species of arachnids are most active during this period of the year (Crawford, 1981; Punzo, 1998b, 2000a). Voucher specimens have been deposited in the Invertebrate Collection of the University of Tampa. Arachnids were located by walking through the site and checking the ground surface, under rocks and plant debris, and rock crevices. Arachnids were also collected using drift fences and pitfall traps as described by Punzo (2000b). To summarise, pitfall traps were 3.0 l plastic buckets, whose lips were positioned flush with the ground surface. Each trap had a white plastic cover placed 3 cm above it to provide shade and protection from rain. Traps were positioned in cross-shaped grids. Each arm of a grid was 12 m in length and consisted of 13 traps. One hundred and forty-five trap grids were established at the site, with each grid separated from another by a minimum distance of 30 m. These collection methods allowed me to record the following data for each animal collected: species identification, sex, total body length (TBL), width of carapace for spiders, whipscorpions and scorpions (CW), width of propeltidium (PW) for solifuges, body weight (BW), time at which the animal was collected or observed active at the ground surface (diel periodicity), and type of microhabitat. Carapace width has been identified as a reliable estimate of growth and body size in spiders (Hagstrum, 1971), whipscorpions (Yoshikura, 1965) and scorpions (Polis & Sissom, 1990), as is propeltidium width in solifuges (Punzo, 1998).

Each arachnid collected or observed was assigned an individual locality using a handheld global positioning system (GPS) receiver. Individual localities were then overlaid on digitised soil and vegetation geographic information system (GIS) layers (Plumb, 1987), provided by the National Park Service, using ArcView GIS 3.2 (Chihuahuan Desert Research Institute, Alpine, Texas, USA).

Measurements of TBL, CW and PW were taken to the nearest 0.1 mm using a dissecting microscope fitted with an ocular micrometer. These morphometric indices also permitted the estimation of age, based on data from previous studies on these or closely related species of arachnids. Body weight was recorded to the nearest 0.1 mg using a portable electronic balance. At all sites at which arachnids were found, including at burrow entrances or in shallow depressions in the ground or under rocks, soil hardness (penetrability) was measured

Species	M	F	I	T
<i>Aphonopelma steindachneri</i>	124	92	47	263
<i>Hogna carolinensis</i>	147	109	216	472
<i>Eremobates palpisetus</i>	83	102	128	313
<i>Mastigoproctus giganteus</i>	101	68	34	203
<i>Diplocentrus bigbendensis</i>	71	55	12	138

Table 1: Number of arachnids ($n=1389$) collected between 10 April and 5 September 2003 at Persimmon Gap in the Chihuahuan Desert. M=males; F=females; I=immatures; T=total.

from the ground surface with a Proctor pocket penetrometer (Model 77114, Forestry Suppliers Inc., Jackson, Mississippi, USA). Hardness values were also recorded at sites throughout the study area. Hardness values were recorded in kg cm^{-2} according to the method of Schraer *et al.* (1998).

Diet composition and temporal patterns of activity

In cases where arachnids were collected with a prey item in their chelicerae, the prey item was removed and placed in 70% ethanol for subsequent taxonomic identification. Following identification, the proportion of prey items from various taxa was determined, and these proportions were used to determine trophic niche breadth using Levin's index (B): $B = 1/\sum p_j^2$, where p_j =proportion of individuals found using a resource (prey item) (Krebs, 1989). The value obtained for B was then standardised using Levin's standardised measure of niche breadth (BA): $BA = B - 1/n - 1$, where n =number of prey types (Krebs, 1989). Values can range from 0 (prey species from only one resource category; narrow niche breadth) to 1 (prey species represented equally in diet; broad niche breadth).

Levin's standardised measure was also used to determine temporal niche breadth for data on the proportion of various arachnids observed active at the ground surface at 2-h time intervals during the course of 24 h (diel periodicity).

Statistical analyses

All statistical tests followed procedures discussed by Sokal & Rohlf (1995). Chi-square goodness-of-fit tests were used to test whether arachnid species were associated with soil and vegetation zones relative to the availability of these habitats according to the digitised soil and vegetation GIS layers described above. Observed frequencies of each arachnid species found on a particular soil type and vegetation zone were compared with expected frequencies based on proportions available within the study site. Habitat availability was determined by dividing the total area (km^2) covered by each soil and vegetative type by the total area of the study site (4.524 km^2).

Data on morphometric indices (TBL, CW, PW and BW) were log-transformed to meet conditions of normality. An analysis of variance (ANOVA) and Scheffe F -tests were used to test for overall effect of sex and life

cycle stage, and to compare means between species, respectively. Student t -tests were used to compare differences within each species.

Differences in proportions of prey items found among the different species of arachnids were tested using a Chi-square contingency test.

Results

A total of 1389 arachnids comprising these 5 species were collected during the course of this study (Table 1). *Hogna carolinensis* comprised 34.0% of all arachnids collected, as compared with 22.5% for *E. palpisetus*, 18.9% for *A. steindachneri*, 14.6% for *M. giganteus*, and 9.9% for *D. bigbendensis*.

Morphometric measurements are shown in Table 2. Sexual size dimorphism was observed for all arachnid species, with females having a larger body size than males. For *A. steindachneri*, 124 of 263 spiders collected were adult males (47.1%), 35.0% females, and 17.9%

Species	TBL (mm)	CW (mm)	BW (g)
<i>Aphonopelma steindachneri</i>			
M ($n=124$)	39.82 ^a (1.02) 37.11–41.14	12.83 ^a (1.69) 10.94–13.38	6.09 ^a (1.05) 4.93–7.88
F ($n=92$)	45.77 ^b (3.81) 41.21–48.16	15.26 ^b (2.04) 13.8–16.7	8.63 ^b (0.89) 7.25–9.76
I ($n=47$)	11.43 ^c (3.98) 4.14–18.31	5.06 ^c (0.61) 2.11–7.74	1.89 ^c (0.38) 0.24–3.62
<i>Hogna carolinensis</i>			
M ($n=147$)	18.02 ^a (2.11) 16.33–20.24	7.93 ^a (1.14) 5.92–8.14	3.28 ^a (0.44) 2.04–4.21
F ($n=109$)	28.34 ^b (4.05) 23.86–32.43	11.11 ^b (2.07) 8.95–12.98	5.16 ^b (0.89) 3.89–6.47
I ($n=216$)	7.81 ^c (1.24) 3.02–13.94	4.96 ^c (0.77) 1.41–6.02	1.26 ^c (0.37) 0.11–2.83
<i>Eremobates palpisetus</i>			
M ($n=83$)	28.28 ^a (2.47) 24.12–32.45	4.01 ^a (0.79) 3.25–5.12	3.02 ^a (0.29) 2.53–3.58
F ($n=102$)	34.83 ^b (3.15) 31.15–38.77	6.13 ^b (1.14) 5.29–7.05	4.77 ^b (0.72) 3.25–5.28
I ($n=128$)	11.54 ^c (1.41) 3.43–18.72	2.21 ^c (0.31) 1.24–3.16	1.72 ^c (0.22) 0.22–2.28
<i>Mastigoproctus giganteus</i>			
M ($n=101$)	38.88 ^a (4.15) 34.3–42.1	11.05 ^a (1.76) 8.23–13.14	3.81 ^a (0.43) 2.87–4.24
F ($n=68$)	44.91 ^b (3.07) 37.32–52.12	15.02 ^b (2.05) 13.24–18.02	5.23 ^b (0.54) 3.86–6.11
I ($n=34$)	19.88 ^c (2.33) 5.32–25.87	6.06 ^c (0.78) 2.87–8.73	1.83 ^c (0.21) 0.28–2.34
<i>Diplocentrus bigbendensis</i>			
M ($n=71$)	36.17 ^a (3.07) 33.47–40.82	11.14 ^a (0.85) 9.21–14.02	3.04 ^a (0.29) 2.43–3.31
F ($n=55$)	42.05 ^b (2.71) 38.84–45.64	15.96 ^b (1.94) 12.89–17.03	5.05 ^b (0.48) 3.88–6.17
I ($n=12$)	15.71 ^c (2.17) 2.89–23.06	4.88 ^c (0.57) 1.53–7.99	1.87 ^c (0.31) 0.17–2.18

Table 2: Measurements of arachnids collected between 10 April and 5 September 2003, at Persimmon Gap in the Chihuahuan Desert. M=males; F=females; I=immatures; TBL=total body length; CW=carapace width, or propeltidium width (PW) for *Eremobates*; BW=body weight. Data expressed as means \pm SE. Numbers below the mean represent the range. Values within columns for each species with different letters are significantly different (t -test, $p < 0.05$).

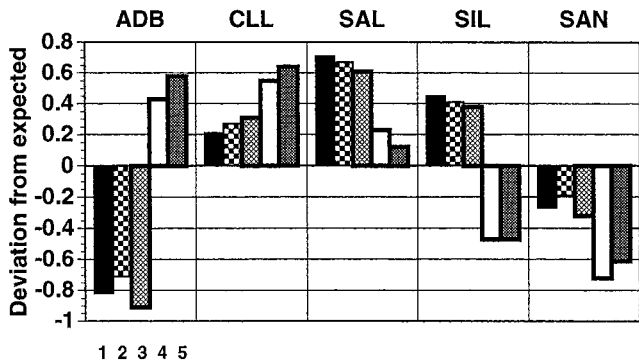


Fig. 1: Deviations of observed versus expected occurrences of individual arachnids of *Aphonopelma steindachneri* (1), *Hogna carolinensis* (2), *Eremobates palpisetulosus* (3), *Mastigoproctus giganteus* (4) and *Diplocentrus bigbendensis* (5), in relation to available soil types: ADB (adobe, 36–39), CLL (clay loam, 9–11), SAL (sand loam, 7–8.9), SIL (silt loam, 3.5–6.5), and SAN (sand, 0.6–2.2). Deviations based on Chi-square goodness of fit of association for all species. Numbers following soil type represent soil hardness values expressed as kg cm^{-2} . Deviations from the expected were scaled from -1 to $+1$ by dividing the greatest deviation from expected (negative or positive) for each species.

immatures. Comparable values were 31.1, 23.1 and 45.8% for *H. carolinensis*, 26.5, 32.6 and 40.9% for *E. palpisetulosus*, 49.8, 33.5 and 16.7% for *M. giganteus*, and 51.4, 39.9 and 8.7% for *D. bigbendensis*.

With respect to associations of arachnid species with soil types and vegetation zones, no significant differences were found between immatures, adult males, or adult females ($p > 0.05$), so data were pooled for statistical comparisons.

Chi-square goodness-of-fit tests showed non-random associations of all species of arachnids across soil types (Fig. 1). Frequencies of each arachnid associated with each soil type are shown in Table 3. Over 41% of all arachnid species were found on sand loam soils, followed by 25.3% (clay loam), 17.8% (silt loam), 9.9% (adobe) and 5.6% (sand). Tarantulas (*A. steindachneri*), wolf spiders (*H. carolinensis*) and solifuges (*E. palpisetulosus*) showed a preference for clay loam, silt loam, and sand loam soils, with relatively few individuals being found on adobe soils.

Soil type (hardness)	Arachnid species				
	AS	HC	EP	MG	DB
Adobe (36–92)	5	8	2	61	61
Clay loam (9–11)	61	131	29	84	46
Sand loam (7–8.9)	110	222	189	35	20
Silt loam (3.5–6.5)	78	66	80	16	7
Sand (0.6–2.2)	9	45	13	7	4

Table 3: Total numbers of individuals of five arachnid species found on specific soil types at Persimmon Gap in Big Bend National Park. Species: AS=*Aphonopelma steindachneri*, HC=*Hogna carolinensis*, EP=*Eremobates palpisetulosus*, MG=*Mastigoproctus giganteus*, DB=*Diplocentrus bigbendensis*. Numbers following soil types are soil hardness values expressed in kg cm^{-2} . No significant differences were found between males, females and immatures (Chi-square goodness-of-fit test, $p > 0.05$), so data are pooled for these life cycle stages for each species.

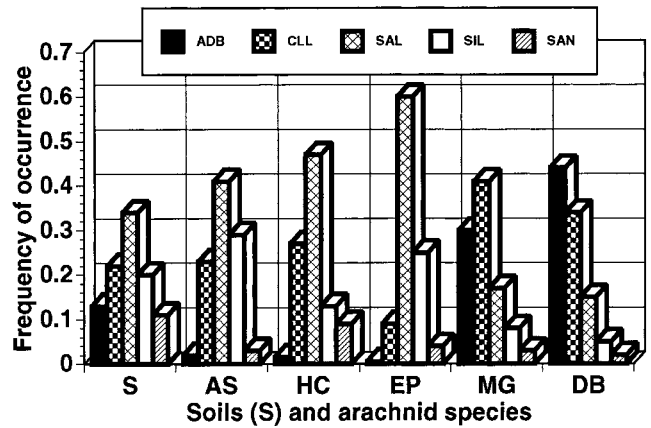


Fig. 2: Frequencies of soil types at Persimmon Gap, Big Bend National Park, and the proportion of the total number of each arachnid species found in the different soil types. Soil types: ADB=adobe, CLL=clay loam, SAL=sand loam, SIL=silt loam, SAN=sand. S=soil type frequency; Arachnid species: AS=*Aphonopelma steindachneri*, HC=*Hogna carolinensis*, EP=*Eremobates palpisetulosus*, MG=*Mastigoproctus giganteus*, DB=*Diplocentrus bigbendensis*.

Frequencies of soil types at Persimmon Gap are shown in Fig. 2. Frequencies of arachnids detected on each soil type relative to the availability of the soil type are also shown. A significantly greater proportion of giant whipscorpions (*M. giganteus*) and scorpions (*D. bigbendensis*) were found on harder adobe soils as compared with the spiders and solifuges ($p < 0.05$). A higher proportion of *H. carolinensis* (9.5%) were found on sandy soils as compared with *A. steindachneri* (3.4%), *E. palpisetulosus* (4.2%), *M. giganteus* (3.4%) and *D. bigbendensis* (2.9%) ($p < 0.05$).

Chi-square goodness-of-fit tests showed a non-random association between all arachnid species and vegetation types (Fig. 3). Six hundred and sixty-three out of 1389 arachnids (47.8%) were found in areas dominated by mixed scrub (Table 4). Out of the 6 vegetation types, most individuals of *A. steindachneri* (48.3%), *H. carolinensis* (59.7%), *E. palpisetulosus*

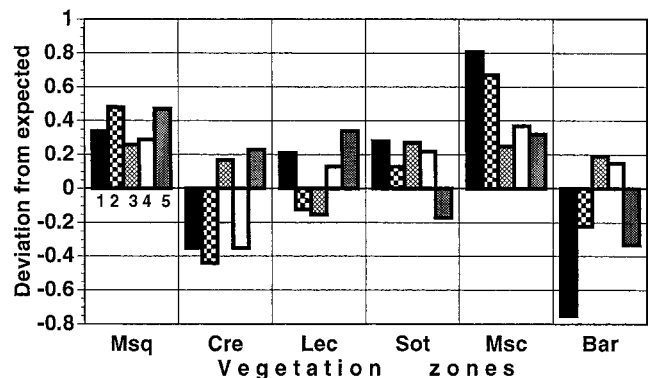


Fig. 3: Deviations of observed versus expected occurrences of individual arachnids of *Aphonopelma steindachneri* (1), *Hogna carolinensis* (2), *Eremobates palpisetulosus* (3), *Mastigoproctus giganteus* (4) and *Diplocentrus bigbendensis* (5), in relation to available vegetation types: Msq=mesquite, Cre=creosote, Lec=lechuguilla, Sot=sotol, Msc=mixed scrub, Bar=barren. Deviations from the expected, based on Chi-square goodness of fit of association for all species, were scaled from -1 to $+1$ by dividing the greatest deviation from expected (negative or positive) for each species.

Vegetation type	Arachnid species				
	AS	HC	EP	MG	DB
Mesquite	57	135	71	60	46
Creosote	9	6	31	6	26
Lechuguilla	24	4	7	21	32
Sotol	41	38	40	33	5
Mixed scrub	127	282	161	66	27
Barren	5	7	3	17	2

Table 4: Total numbers of individuals of five arachnid species found in specific vegetation types (zones) at Persimmon Gap in Big Bend National Park. AS=*Aphonopelma steindachneri*, HC=*Hogna carolinensis*, EP=*Eremobates palpisetulosus*, MG=*Mastigoproctus giganteus*, DB=*Diplocentrus bigbendensis*. No significant differences were found between males, females and immatures (Chi-square goodness-of-fit test, $p > 0.05$), so data are pooled for these life cycle stages for each species.

(51.4%) and *M. giganteus* (32.5%) were associated with mixed scrub (Table 4). In contrast, most scorpions (*D. bigbendensis*) were associated with mesquite (33.3%) and lechuguilla (23.2%), with only 19.6% found in mixed scrub zones.

Prey items were found only for adult arachnids. No differences were found for diet composition between sexes for any arachnid species ($p > 0.05$). Total numbers of prey found for each arachnid were: 157 (*A. steindachneri*), 282 (*H. carolinensis*), 89 (*E. palpisetulosus*), 211 (*M. giganteus*) and 136 (*D. bigbendensis*). Prey items found in the chelicerae of these arachnids indicate that they are generalist predators and feed on a wide variety of ground-dwelling arthropods at Persimmon Gap (Fig. 4). With respect to insects, beetles (Coleoptera) comprised between 11 and 31% of the prey items for these arachnids, followed by orthopterans (7–23%), caterpillars (Lepidoptera, 1–30%), hemipterans (2–7%)

and cockroaches (Blattaria, 0–6%). For arachnids, values were: spiders (7–18%), scorpions (4–8%) and solifuges (6–15%). Spiders captured as prey included immature and adult wolf spiders (Lycosidae), lynx spiders (Oxyopidae), gnaphosids, amaurobiids, araneids, clubionids, and immature tarantulas (Theraphosidae). None of the arachnids was found with a whipscorpion in its chelicerae. Values for Levins' measurement of trophic niche breadth were: 0.4583 (*A. steindachneri*), 0.4424 (*H. carolinensis*), 0.4288 (*E. palpisetulosus*), 0.4508 (*M. giganteus*), and 0.3887 (*D. bigbendensis*).

Temporal patterns of activity are shown in Fig. 5 and indicate that all of these arachnid species exhibited a strong tendency toward nocturnal activity during mid-spring to late summer. No significant differences were found between immatures and adults for any arachnid species ($p > 0.05$). No individuals of *A. steindachneri* were observed active at the ground surface between 0800 and 1559h (Central Standard Time, CST). No activity was observed for *E. palpisetulosus* and *D. bigbendensis* between 0800 and 1759h, for *H. carolinensis* between 1200 and 1559h, and *M. giganteus* between 1000 and 1559h. Seventy-seven percent of individuals of *A. steindachneri* were active between 2200 and 0359h. Comparable values for the same time period were 72% for *D. bigbendensis*, 70% for *E. palpisetulosus*, 45% for *H. carolinensis*, and 43% for *M. giganteus*. Individuals of *H. carolinensis* became active earlier in the day than the other arachnids, with 5% active between 0800 and 0959h, and 12% between 1600 and 1759h. Eight and 14%, respectively, of individuals of *M. giganteus* and *D. bigbendensis* were active around dawn (0600–0759h), as compared with only 0–2% for the other arachnids. Values for Levins' measurement of temporal niche breadth were: 0.5821 (*A. steindachneri*), 0.5521 (*H.*

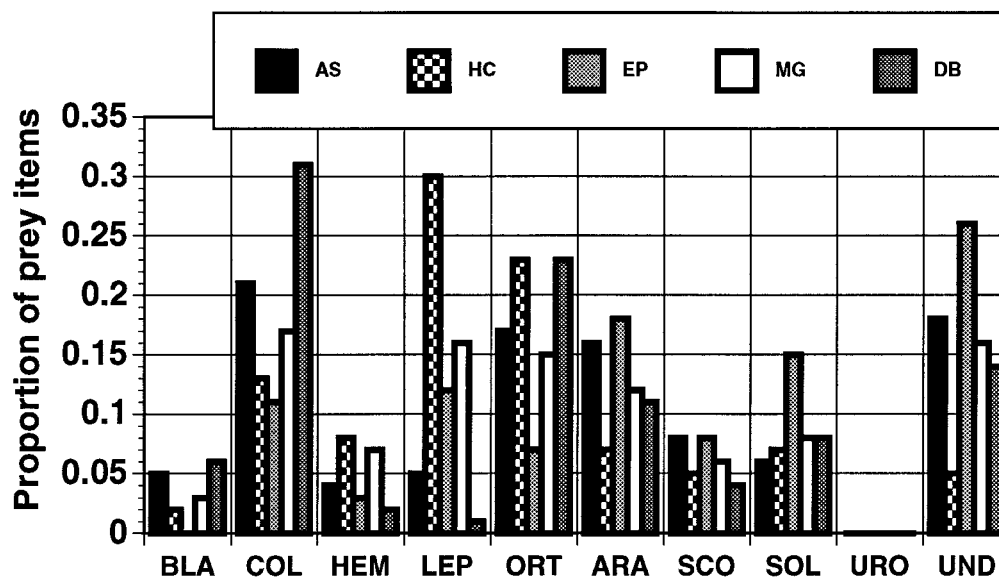


Fig. 4: Proportions of different types of prey items found in chelicerae of adult arachnids from Persimmon Gap, Big Bend National Park. AS=*Aphonopelma steindachneri*; HC=*Hogna carolinensis*; EP=*Eremobates palpisetulosus*; MG=*Mastigoproctus giganteus*; DB=*Diplocentrus bigbendensis*. Prey items were identified to order: BLA=Blattaria: cockroaches, COL=Coleoptera: beetles, HEM=Hemiptera: bugs, LEP=Lepidopteran larvae, ORT=Orthoptera: grasshoppers, katydids, etc., ARA=Araneae: spiders, SCO=Scorpiones: scorpions, SOL=Solifugae: solifuges, URO=Uropygi: whipscorpions, UND=unidentified arthropods. No prey items were found in the chelicerae of immature arachnids. Data pooled for male and female arachnids because no significant differences were found between sexes (Chi-square contingency test, $p > 0.05$).

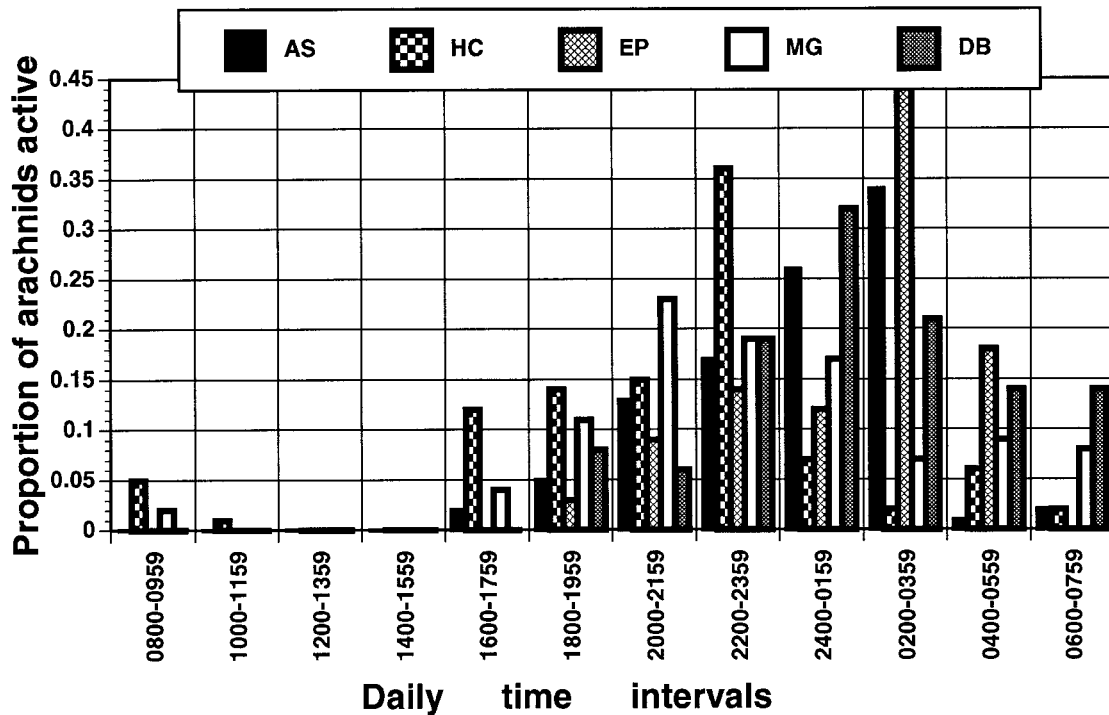


Fig. 5: Proportion of arachnids active at various daily time intervals Persimmon Gap, Big Bend National Park). AS=*Aphonopelma steindachneri*; HC=*Hogna carolinensis*; EP=*Eremobates palpisetulosus*; MG=*Mastigoproctus giganteus*; DB=*Diplocentrus bigbendensis*. No significant differences were found between immatures and adults ($p>0.05$), so data are pooled for all arachnid species.

carolinensis), 0.4983 (*E. palpisetulosus*), 0.4637 (*M. giganteus*) and 0.5057 (*D. bigbendensis*).

Discussion

Wolf spiders represented the arachnid species most frequently collected at Persimmon Gap (PG) during the course of this study, followed by solifuges, tarantulas, giant whipscorpions and scorpions. Adult females were larger than males for all the arachnid species, which is in agreement with previous studies on body size in *A. steindachneri* (Smith, 1994), *H. carolinensis* (Shook, 1978; Punzo, 2003), *E. palpisetulosus* (Punzo, 1995), *M. giganteus* (Cloudsley-Thompson, 1991; Punzo, 2000b), and *D. bigbendensis* (Polis & Sisson, 1990) from desert regions in the USA.

Additionally, the results indicate that environmental factors such as type of soil and vegetation play an important role in determining choice of microhabitats by these arachnids. Data are available for relatively few species with respect to relationships between soil type (hardness) and distribution of arthropods in BBNP (Punzo, 1998a). Tarantulas, wolf spiders and solifuges were most commonly associated with clay loam, silt loam, or sand loam soils, whereas a higher proportion of whipscorpions and scorpions were found on harder adobe soil in addition to clay loam. This suggests that the stout and heavily sclerotised pedipalps of *M. giganteus* (Weygoldt, 1971) and *D. bigbendensis* (Hjelle, 1990) allow these arachnids to utilise (construct burrows in) harder soils. At PG, *E. palpisetulosus* was most commonly found on sand loam soils, which is in agreement with results reported for this solifuge from other areas of Trans Pecos Texas (Punzo, 1998b), as well as

for another sympatric solifuge, *E. marathoni* (Punzo, 1995).

Only a small proportion of individuals of *M. giganteus* were found on sandy soil at PG (3.4%), as compared with its more frequent use by adults (25–30%) at other sites in BBNP that were rockier and at higher elevations (Punzo, 2001). Burrows of females of another tarantula species found within the Park (*Aphonopelma hentzi* (Girard)) were more frequently associated with softer silt loam and sandy soils (Punzo & Henderson, 1999) as compared with *A. steindachneri*, suggesting that differences in substrate preference may reduce competition between these two theraphosids.

All species were found more frequently than expected at sites where mesquite and mixed scrub were dominant. Tarantulas and wolf spiders were found less frequently than expected in barren areas, or those characterised by creosote. Scorpions were also found less frequently than expected in barren areas. Tarantulas, whipscorpions and scorpions were found more frequently in areas with lechuguilla, and wolf spiders and solifugids less frequently. In BBNP lechuguilla is often associated with sites that have drainage patterns associated with steep inclines and rockier substrates, which may present more of an obstacle for burrowing in some of these arachnids. Other BBNP animals whose survival depends on fossorial behaviour have been shown to occur in smaller numbers in lechuguilla-dominated areas, including frogs and toads (Dayton & Fitzgerald, 2001), millipedes (Crawford, 1981), and centipedes (Cloudsley-Thompson, 1991). Although mixed scrub sites were positively associated with most of these arachnids, it is difficult to gauge the extent to which vegetation types influence arachnid distribution patterns because of the

relationship between vegetation and soil type. Previous studies have suggested that in desert regions, soil type plays a more important role in determining microhabitat utilisation in arthropods than vegetation type (see reviews by Crawford, 1981; Polis, 1990; Punzo, 2000a). In general, no single biotic or abiotic factor alone can be expected to determine species persistence across a variety of landscapes. For desert arthropods that rely on some degree of fossoriality for survival, substrates that allow animals to find shelter and excavate burrows/nests with minimal energy expenditure should be favoured over less optimal substrates.

Similarity in diet composition, coupled with the fact that these arachnids are typically active at night, suggests that these arachnid species compete with one another for food. Contents of the chelicerae as well as trophic niche breadth indicate that these arachnids feed on a wide variety of ground-dwelling arthropods. The existence of intraguild predation is supported by the fact that 19–41% of prey items consisted of spiders (including theraphosids), scorpions or solifuges. Although giant whipscorpions included tarantulas, wolf spiders, scorpions, and solifuges in their diet, they were notably absent from the diets of the other arachnids, probably because they possess a strong chemical defence in the form of repellent secretions (Eisner, 1970).

In conclusion, these results indicate that *A. steindachneri*, *H. carolinensis*, *E. palpisetulosus*, *M. giganteus* and *D. bigbendensis* all feed on a similar variety of arthropods and in general prefer similar vegetation types. Additionally, all species were strongly nocturnal in their diel periodicity, and all were strongly associated with sand loam and/or clay loam soils. As a result, these arachnid species are potential competitors for food and shelter sites at Persimmon Gap in BBNP.

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