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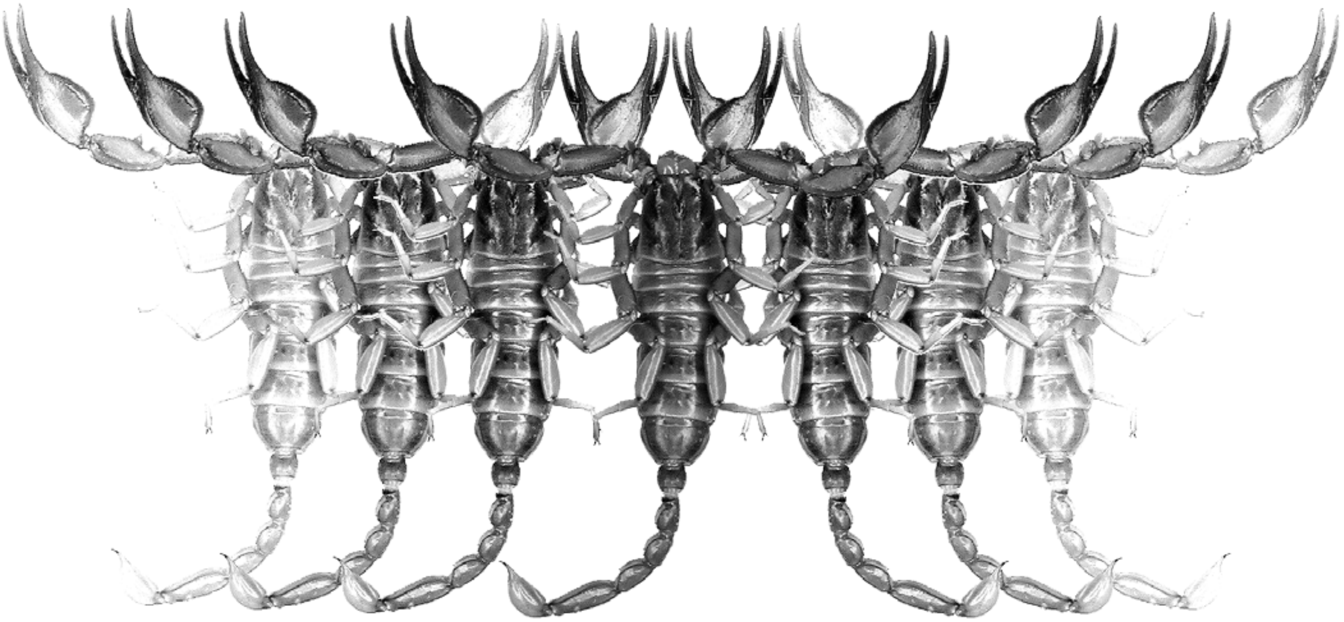

Ontogenetic Shifts in Microhabitat Use, Foraging and Temporal Activity for the Striped Bark Scorpion *Centruroides vittatus* (Scorpiones: Buthidae)

C. Neal McReynolds

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Ontogenetic shifts in microhabitat use, foraging and temporal activity for the striped bark scorpion *Centruroides vittatus* (Scorpiones: Buthidae)

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Summary

Ontogenetic shifts in activity and habitat use by the scorpion *Centruroides vittatus* in Laredo, Texas can occur with shifts in microhabitat use, the height of the scorpion in vegetation and seasonal and lunar activity among different sizes of *C. vittatus* but not taxa of prey in the diet. The microhabitat use by the different size classes was significantly different with significant associations among the cacti with a high frequency of larger scorpions on prickly pear cactus and strawberry cactus and between grass and other vegetation with a high frequency of smaller scorpions on grass. A comparison of the mean height of scorpion on blackbrush among the size classes was not significant but height on grass was significant. The activity of the size classes was significantly different among months and lunar cycle. Temperature had a significant effect on the activity of scorpions by different size classes and in different microhabitats. Caterpillar availability did not have a significant association with either scorpion size class or microhabitat use by scorpions. The taxa of prey captured by the different size classes were not significantly different including no notable difference in scorpions feeding on caterpillars. The size classes of *C. vittatus* show microhabitat and temporal shifts in activity. The results suggest that smaller scorpions can possibly be avoiding the larger scorpions by reducing activity in the preferred microhabitat (prickly pear and strawberry cactus) of larger scorpions.

Introduction

Size (or age) can influence activity and habitat use by an individual scorpion (see Polis, 1984, 1988a). Scorpions have direct development with the juvenile resembling a miniature adult, and the different sizes (and ages) can overlap over time (a size-structured population: see Polis, 1988a). During development, ontogenetic shifts in behavior can occur because the optimal behavior is size-dependent or because tradeoffs due to interactions with the biotic environment are size-dependent (e.g., tradeoff between growth rate determined by foraging success and mortality rate determined by predation: see Werner & Hall, 1988). Taxa with direct development and size-structured populations have ontogenetic shifts in behavior including habitat shifts (see Mittelbach, 1984; Werner & Hall, 1988) and changes in foraging behavior (see Cisneros & Rosenheim, 1997; Svanbäck & Persson, 2004; Rudolf, 2006).

Shifts in activity with an increase in size (and age) can be due to the following alternate hypotheses. (1) The shifts can be due to ontogenetic differences in diet (Smith & Petranka, 1987; Cisneros & Rosenheim, 1997) and preferred habitat for foraging (Ehlinger & Wilson, 1988; Ehlinger, 1990; Arakaki & Tokeshi, 2005). (2) The shifts can be due to changes in risk from predators at different sizes (Werner, 1988; Werner & Hall, 1988). The size class most vulnerable to predation can shift from an optimal to a sub-optimal habitat when predation risk is high (Werner & Hall, 1988; Gilliam & Fraser, 1988; Resetarits, 1995). Once an individual has grown to a size that is less vulnerable to predation the individual can shift to habitat with higher predation risk (Gibson et al., 2002). However, risk of predation does not always cause habitat shift if prey can find a refuge within the habitat as in crab spiderlings hiding in an inflorescence from jumping spiders (Morse, 2007). (3) If size classes are interacting by exploitation competition, interference competition or cannibalism, then this can cause temporal or habitat shifts (Polis, 1988a; Rudolf, 2007; Rudolf & Armstrong, 2008). The sizes most vulnerable to cannibalism can shift habitat or temporal activity (Murdoch & Sih, 1978; Sih, 1981, 1982). Larger or older individuals can exclude smaller or younger individuals from the habitat with lower risk of predation (Cresswell, 1994). This can cause a shift in diet as well because of differences in availability of prey in the sub-optimal time or habitat (Polis, 1980a, 1984; Polis & McCormick, 1986).

Examples of scorpion size (and age) influencing activity and microhabitat use include: In the sand scor-

Figure 1: *Centruroides vittatus* on the trunk of blackbrush (A. rigidula) fluorescing under ultraviolet light.

pion, *Smeringurus* (formerly *Paruroctonus*) *mesaensis* (Stahnke, 1957) (fam. Vaejovidae), age affects surface activity over time (Polis, 1980a), foraging (Polis, 1984, 1988b), cannibalism as prey or predator (Polis, 1980b), intraguild predation as prey or predator (Polis & McCormick, 1987) and home range size (Polis et al., 1985). Juveniles can climb more in vegetation than adults in *Paruroctonus utahensis* (Williams, 1968) (Vaejovidae) and *Buthus occitanus* (Amoreux, 1789) (Buthidae) (Bradley, 1988; Skutelsky, 1996). A temporal shift in activity between juveniles and adults can occur with lunar cycle in *B. occitanus* (Skutelsky, 1996), but temporal shifts between adults and juveniles do not always occur as in *P. utahensis* (Bradley, 1988). In earlier studies of the focal animal, *Centruroides vittatus* (Say, 1821) (Buthidae), more juveniles than adults were observed climbing in vegetation (Brown & O'Connell, 2000), and temporal differences in surface density occur in adults, juveniles and second instars (Yamashita, 2004). Parameters such as microhabitat use, taxa of prey in the diet, the height of scorpion in vegetation and seasonal and lunar activity have been examined in previous studies (see McReynolds, 2004, 2008), but the size of scorpion was not considered. In this study, these parameters will be compared among size classes of *C. vittatus* (Fig. 1).

Two environmental factors influence *S. mesaensis* activity of different ages: temperature (Polis 1980a) and prey abundance (Polis, 1980a, 1988b). Intermediate age scorpions have high activity at lower temperatures and low activity at higher temperatures where adults and the youngest scorpions are more active (Polis, 1980a). An increase in prey abundance can increase the foraging activity of adult *S. mesaensis* but not change or decrease activity for younger scorpions (Polis, 1980a, 1988b). One hypothesis on how temperature could affect microhabitat use by *C. vittatus* is that cacti are diurnal refuges and scorpions are found on cacti at higher frequencies at high and/or low temperatures when the cacti buffer the extreme temperatures (McReynolds, 2008). The microhabitat used for foraging by *C. vittatus* could be influenced by prey availability in the microhabitat (see Polis, 1980a, 1988b). In this study, the availability of caterpillars in blackbrush (*Acacia rigidula*) will be con-

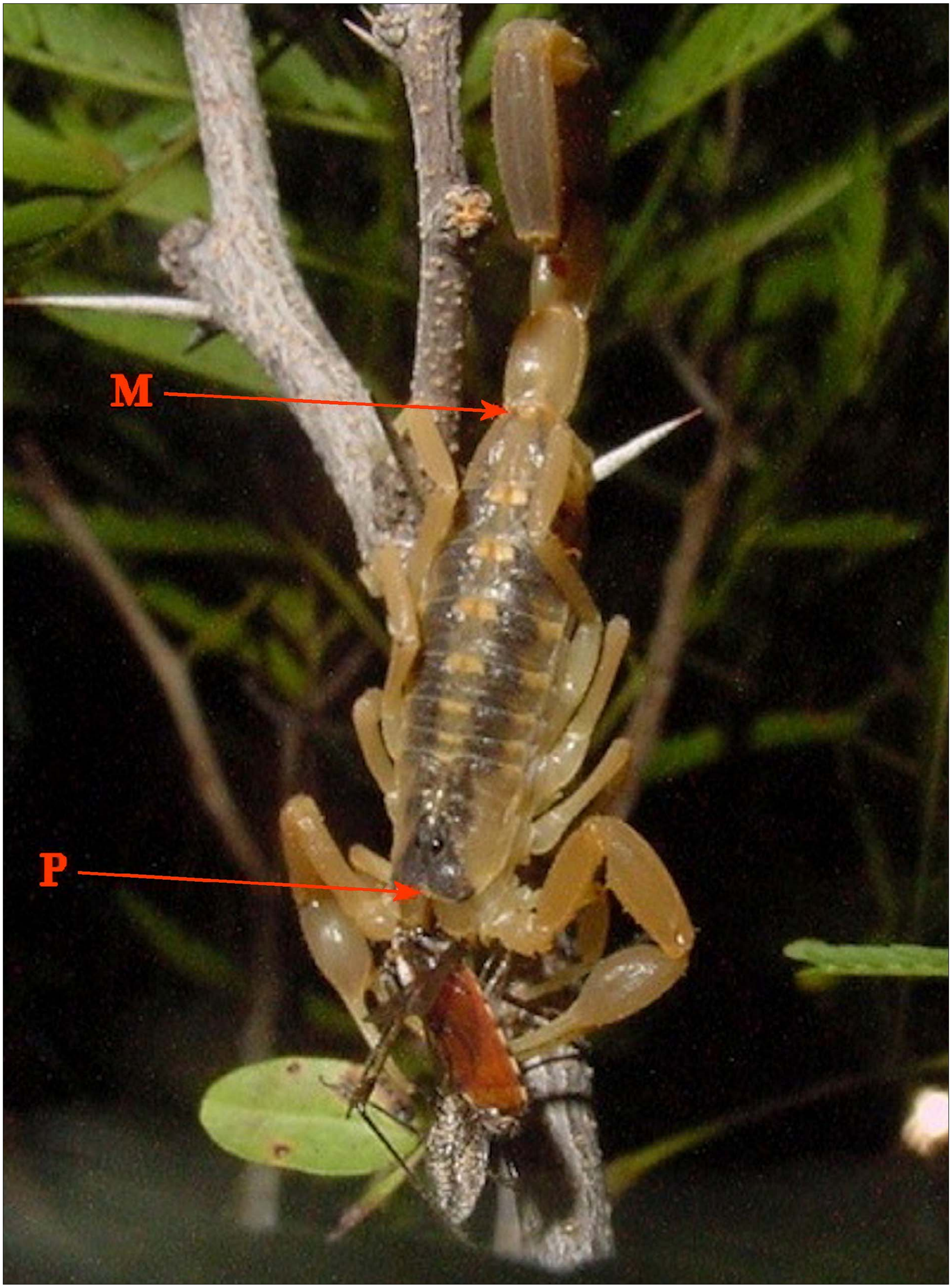

Figure 2: *Centruroides vittatus* length estimated from length of the scorpion from the anterior of the prosoma (P) to the posterior of the mesosoma (M).

sidered. Caterpillars are important prey items for *C. vittatus* in South Texas, and scorpions are often observed feeding on caterpillars in blackbrush (McReynolds, 2004, 2008). Ontogenetic shifts in diet and microhabitat use (especially blackbrush) with caterpillar availability could indicate support for either the first hypothesis or the third hypothesis from above. If the smaller are foraging in blackbrush and have a high frequency of caterpillars in the diet, then this would support hypothesis one. If the larger scorpions are foraging in blackbrush and have more caterpillars in the diet, then this could support the first hypothesis but could support the third hypothesis if larger scorpions are excluding smaller scorpions from blackbrush and denying smaller scorpions access to caterpillars.

This study was done to test whether there are any ontogenetic shifts in microhabitat use and the activity of *C. vittatus*. The microhabitat use among different size scorpions will be compared to determine if there are ontogenetic shifts for certain microhabitats such as blackbrush, prickly pear cactus and/or strawberry cactus. Height of scorpions in vegetation will be compared between different size scorpions to determine if smaller size scorpions climb higher in vegetation. Temporal patterns (monthly or lunar phases) will be compared among different size scorpions to determine if there are temporal shifts. Two factors, temperature and prey (caterpillar) availability, will be compared among different size scorpions and microhabitats. In addition, the type of prey captured among different size classes will be compared to determine possible ontogenetic shifts in foraging.

Methods

Study animal. Centruroides vittatus is widely distributed from northern Mexico to central United States (Shelley & Sissom 1995). *C. vittatus* is nocturnal with refuges during the day in debris, beneath vegetation, under bark, and in holes in the ground, but *C. vittatus*, like other bark scorpions, rarely dig their own burrows (Polis, 1990). Scorpions emerge from their refuge only occasionally to forage (Polis, 1980a; Bradley, 1988; Warburg & Polis, 1990). Scorpions of different sizes can be observed throughout the year with birth in *C. vittatus* occurring between April and September and an age of maturity between 36 and 48 months (Polis & Sissom, 1990). On nights of emergence, *C. vittatus* is active on the ground and/or in vegetation. Courtship by *C. vittatus* has rarely been observed and females carrying first instars observed only occasionally in the field (pers. obs.). Voucher specimens of *C. vittatus* (3 males, 4 females and 2 juvenile scorpions) were deposited in the invertebrate collection at Texas A&M International University.

Habitat. This study was done on the campus of Texas A&M International University (27°35’ N, 99°26’ W), Laredo, Texas, USA, that is in the southern end of the distribution of *C. vittatus.* Laredo is in the Tamaulipan Biotic Province that is characterized by low precipitation and high average temperatures (Blair 1950). Thorny brush (or chaparral) is the habitat of the research plots (Blair 1950). Vegetation in the plots included blackbrush (*Acacia rigidula*), guajillo (*Acacia berlandieri*), honey mesquite (*Prosopis glandulosa*), Texas prickly pear cactus (*Opuntia engelmannii*), tasajillo (*Opuntia leptocaulis*), strawberry cactus (*Echinocereus enneacanthus*), cenizo (*Leucophyllum frutescens*), guayacan (*Guaiacum angustifolium*), leather stem (*Jatropha dioica*), lotebush (*Ziziphus obtusifolia*), Spanish dagger (*Yucca treculeana*), and other plant species.

Data collection. Scorpions were observed at night by locating scorpions fluorescing under ultraviolet light (Stahnke, 1972; and see Sissom et al., 1990). Ground and vegetation were searched by shining the fluorescent light over the area. Observed scorpions were active and either out of their refuges or just emerging. No data were collected on scorpions in their refuges to avoid destruction of the habitat. Data on scorpion size classes for most of the comparisons were collected from September 2, 2003 to November, 15 2005 over 150 nights. Data on caterpillar availability was collected from May 20, 2004 to May 12, 2005 over 70 nights and September 12, 2006 to September 10, 2007 over 47 nights and then compared to scorpion data collected on the same nights. Scorpion data were collected after sunset between 19:30 Central Standard Time, U.S. (CST) at the earliest and 01:00 CST at the latest for an average of two hours per night of observation. Sites were selected at random and searched during a night of observation with a mode of three sites searched per night. Sites were 100 m^2 but the area outside the sites were searched for scorpions and included in this data. One reason for these extended searches is to reduce an edge effect when spatial analyses are performed on this data. The total area searched during the night was not determined for this study and varied from night to night depending on personnel.

All months were sampled, but scorpions were rarely active during December and January. Scorpions can be active during all other months especially when the temperature is above 20° C during the night. Air temperature data was collected each night using a portable weather meter, Kestrel® 3000. During the nights in the field, the phase of the lunar cycle, the percentage of illumination on the moon and time of moon rise or moon set were determined using the data for Laredo, Texas USA from the Complete Sun and Moon Data for One Day: U.S. Cities and Towns from United States Naval

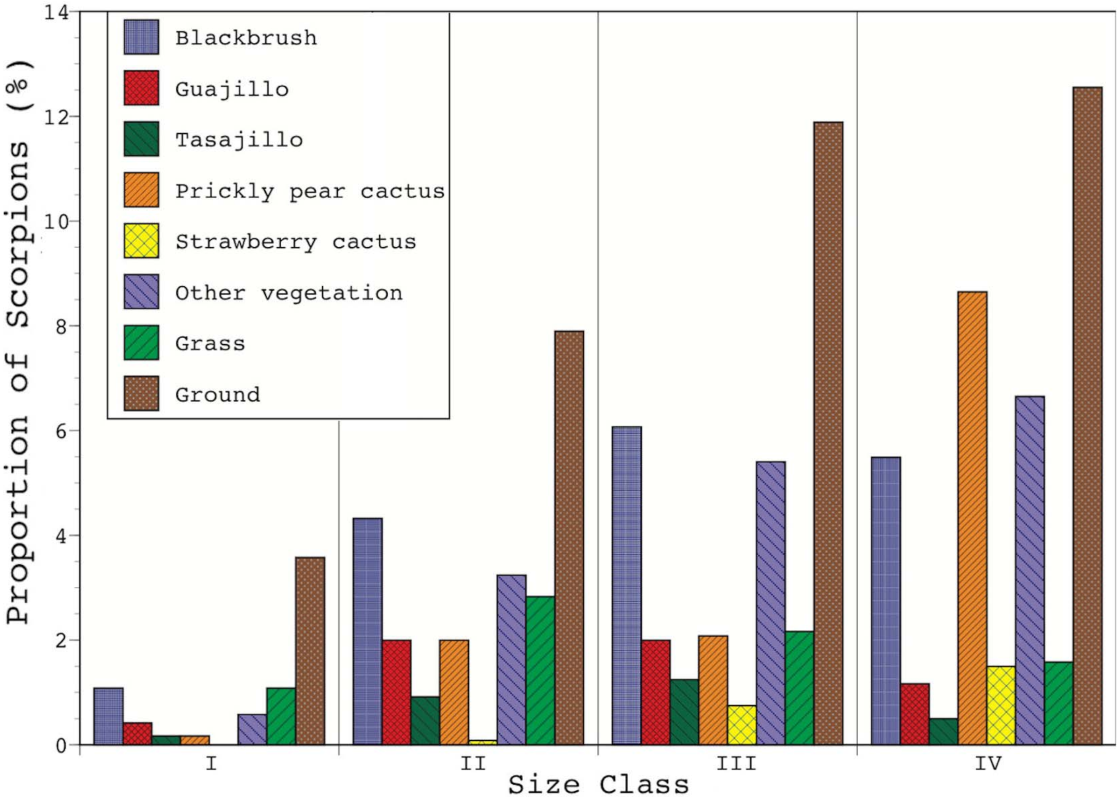

Figure 3: The proportion (%) of *C. vittatus* using different microhabitats among scorpion size classes. Size classes I and II were pooled for the statistical analysis. The frequency of scorpions for different microhabitats was significantly different among size classes (G = 113.544, P < 0.001, df = 14, n = 1203). See Table 1 for planned comparisons among microhabitats.

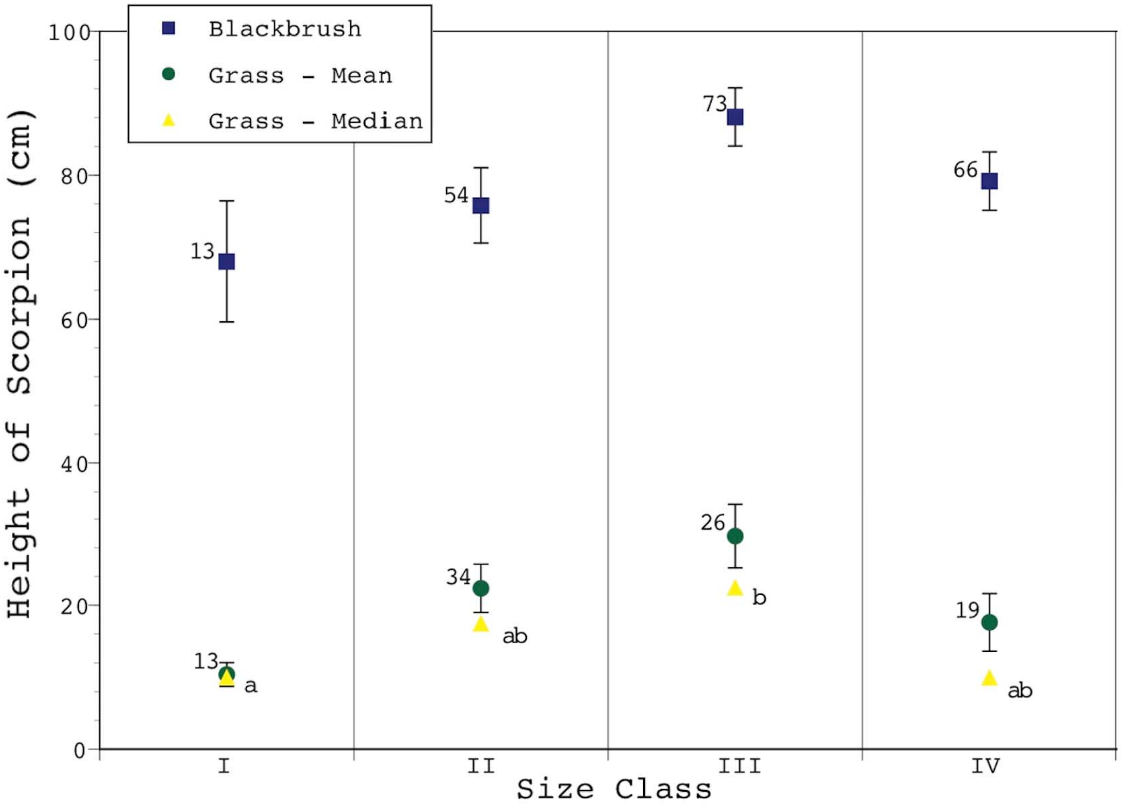

Figure 4: The mean height of *C. vittatus* on blackbrush and grass among scorpion size classes and median for grass. Standard error bar (± 1 SE) and sample size (n) were shown for the mean of each class. Mean scorpion height on blackbrush was not significantly different among size classes (ANOVA: F(3.202) = 2.066), but median scorpion height on grass was significantly different among size classes (Kruskal-Wallis Statistic: KW = 11.551 (corrected for ties), P < 0.01). Medians with the same letter were not significantly different in unplanned comparisons using Tukey-Kramer's multiple tests.

Planned Comparisons	***G***	***df***	***P***
Ground vs. Vegetation	2.796	2	ns
***Acacia* vs. Cacti vs. Grass + Other vegetation**	48.376	4	P < 0.001
Tasajillo vs. Prickly pear cactus vs. Strawberry cactus	35.822	4	P < 0.001
Blackbrush vs. Guajillo	4.224	2	ns
Other vegetation vs. Grass	22.325	2	P < 0.001
Total	113.544		P < 0.001

Table 1: Planned comparisons among microhabitats of the contingency table for microhabitats vs. scorpion size classes. All scorpions using vegetation were pooled for the first comparison vs. scorpions on the ground. Scorpions were pooled in three microhabitat classes for the second comparison: *Acacia* spp. (blackbrush and guajillo) vs. cacti (tasajillo, prickly pear cactus and strawberry cactus) vs. grass plus other vegetation. ns = not significant. See Fig. 3.

Planned Comparisons	***G***	***df***	***P***
J-A vs. M-A vs S-D	57.302	4	< 0.001
J-F vs. M vs. A	28.864	4	< 0.001
M vs. J vs. J vs. A	21.961	6	< 0.01
S vs. O vs. N-D	8.999	4	ns
Total	117.126	18	< 0.001

Table 2: Planned comparisons among months of the contingency table for months vs. scorpion size classes. Months of the year in order with January and February pooled as J-F and November and December as N-D. Months were pooled for the first comparison with January to April (J-A) vs. May to August (M-A) vs. September to December (S-D). ns = not significant. See Fig. 5.

Observatory (http://www. usno.navy.mil/ USNO/ astronomical-applications/data-services/rs-one-day-us). For data analysis, the observations of each scorpion during the night were placed in 6 classes based on the four phases of the lunar cycle and whether the moon was set or risen.

The same data were collected for all scorpions observed during the night in or near the site. These data included date and time of observation, species of scorpion, size class of scorpion (see below), microhabitat used, height of scorpion in vegetation, if scorpion had captured prey or not and prey taxa. The microhabitat use observed for each scorpion was recorded in the field as on the ground or species of vegetation. The microhabitat classes for the contingency table included: ground, grass, blackbrush, guajillo, prickly pear cactus, tasajillo, strawberry cactus, and other vegetation. If observed on soil, leaf litter, or a rock, the scorpion was considered on the ground. Grasses were not identified to species, but all other plants were identified to species if possible. The other perennial shrubs listed above in Habitat were pooled into the other vegetation class. Prey capture classes included no prey captured, caterpillars (Lepidoptera larvae), other insects (including adult Lepidoptera) and IGP (intraguild prey including Scorpiones, Araneae, Solifugae, Opiliones and Chilopoda). Prey captured by scorpions can be observed as scorpions digest externally, thus prey items can be observed in pedipalps or chelicerae (Polis 1979).

Size Classes. The size of *C. vittatus* was estimated as size classes. The age classes for *S. mesaensis* were estimated by a similar manner (Polis, 1980a, 1984; Polis et al., 1985). A visual estimate of the length of the scorpion from the anterior of the prosoma to the posterior of the mesosoma (Fig. 2 and see Polis & McCormick, 1987) was used to place each observed scorpion in one of four size classes. Size class I was < 5 mm and included second instars which recently dispersed from the dorsal mesosoma of the female. Size class II was between 5-10 mm and size class III between 10-15 mm. Size class IV was > 15 mm and included primarily adult males and females but some penultimate instars were also included in this size class. The numbers of instars are between 7 and 9, and estimate of age to maturity is 36 to 48 months for *C. vittatus* (Polis & Sissom, 1990). However, the specific age or instar of a scorpion in any size class cannot be determined at this time for *C. vittatus* in south Texas because the life history of *C. vittatus* has not been described for south Texas.

Caterpillar Availability. The relative caterpillar availability was estimated by randomly sampling blackbrush at different locations each night (Quintanilla, 2008). A standardized collection involved the use of a canvas beating sheet (from Bioquip) that was situated

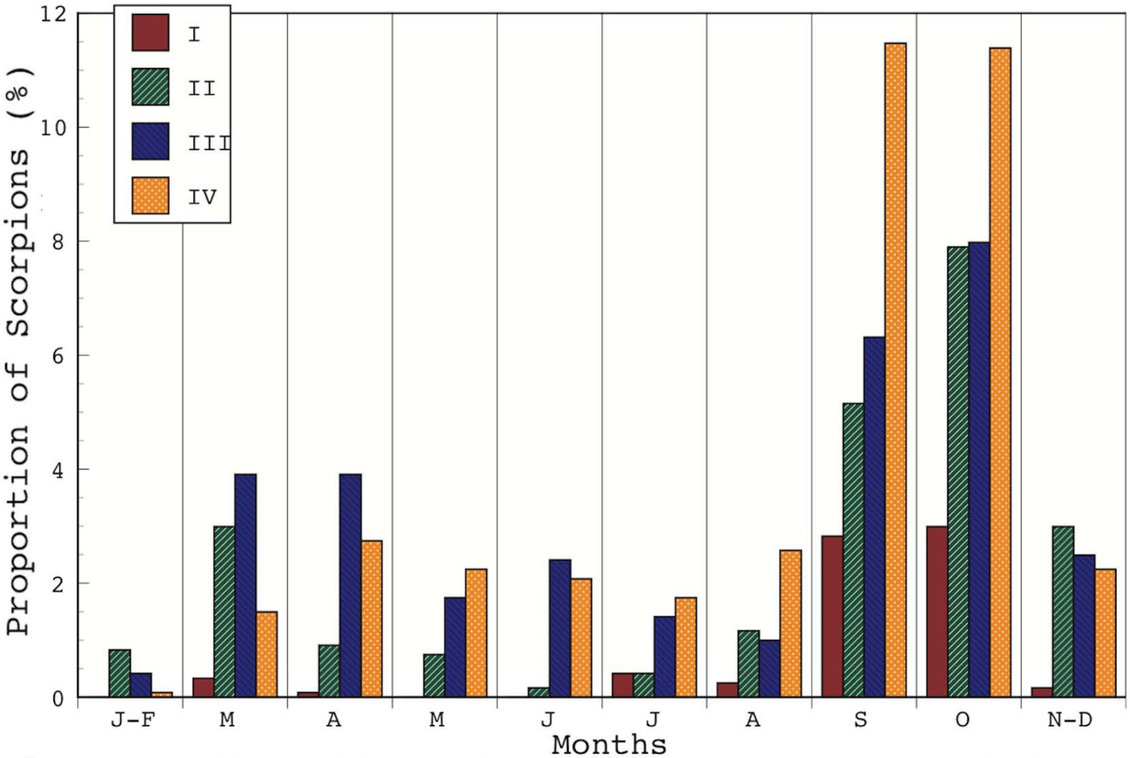

Figure 5: The proportion (%) of *C. vittatus* during different months among scorpion size classes. Months of the year in order with January and February (J-F) and November and December (N-D) pooled. Size classes I and II were pooled for the statistical analysis. The frequency of scorpions during different months was significantly different among size classes ($G = 117.126$, $P < 0.001$, $df = 18$, $n = 1203$). See Table 2 for planned comparisons among months.

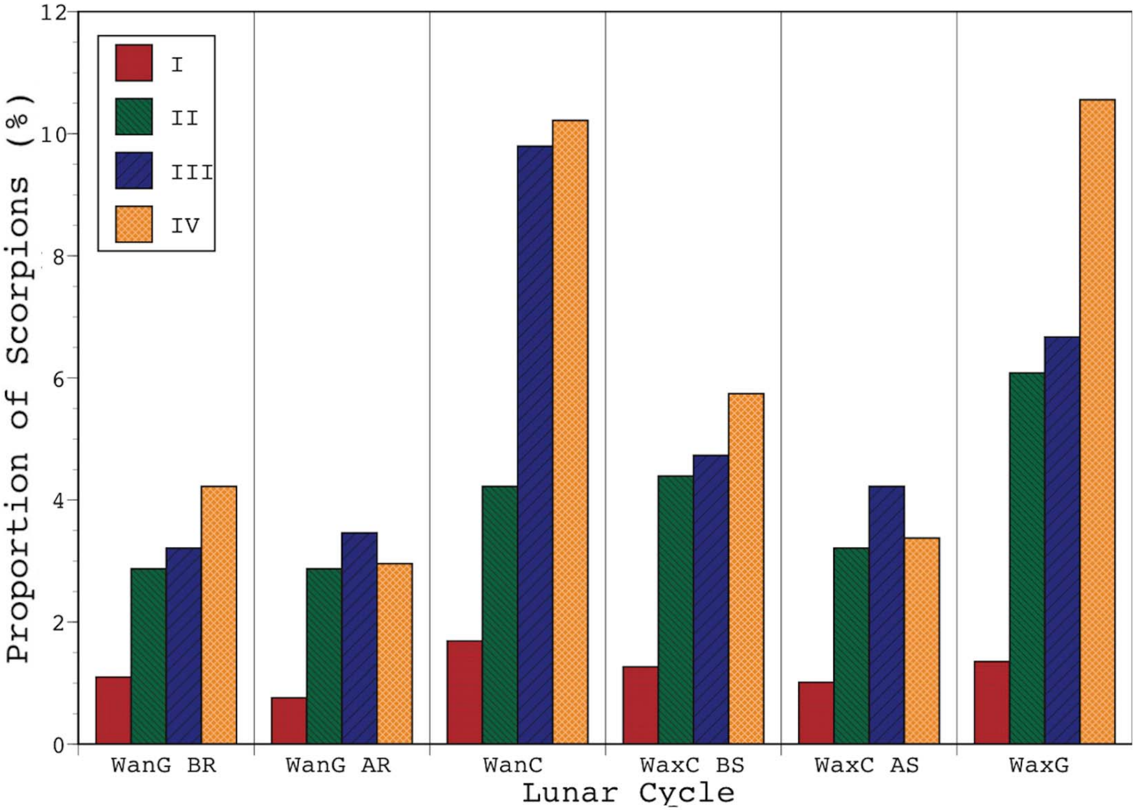

Figure 6: The proportion (%) of *C. vittatus* during the lunar cycle among scorpion size classes. For the comparison, the lunar cycle was divided into the four phases and whether the moon had already set or risen (total of 6 classes): Waning gibbous before moon rise (WanG BR), Waning gibbous after moon rise (WanG AR), Waning crescent (WanC), Waxing crescent before moon set (WaxC BS), Waxing crescent after moon set (WaxC AS) and Waxing gibbous (WaxG). The frequency of scorpions during the phases of the lunar cycle was significantly different among size classes ($G = 29.270$, $P < 0.05$, $df = 15$, $n = 1184$). See Table 3 for planned comparisons among phases of the lunar cycle.

Planned Comparisons	*G*	*df*	*P*
No moon vs. ≤ 50% vs. > 50%	8.407	6	ns
No moon	14.138	6	< 0.05
> 50 %	6.725	3	0.1 > P > 0.05
Total	29.270	15	< 0.05

Table 3: Planned comparisons among phases of the lunar cycle for the contingency table of lunar cycle vs. scorpion size classes. Planned comparisons were based on the amount of illumination during observation of scorpion with the first comparison between no moon present (0% illumination for waning crescent, waxing crescent after moon set and waning gibbous before moon rise), < 50% of the moon illuminated (waxing crescent before moon set) and > 50% of the moon illuminated (waning gibbous after moon rise and waxing gibbous); the second comparison between phases with no moon present (waning crescent vs. waxing crescent after moon set vs. waning gibbous before moon rise); and the third comparison between phases with > 50% of the moon illuminated (waning gibbous after moon rise vs. waxing gibbous). ns = not significant. See Fig. 6.

under the tree canopy, to collect potential prey items that were dislodged from the blackbrush by shaking branches. The specimens were collected from the beating sheets with an aspirator, preserved in ethanol, and the number of caterpillars and other prey were counted for each sample (Quintanilla, 2008). The mean number of caterpillars collected per sample was calculated for each night and compared to microhabitat use and scorpion size classes observed during that night.

Data analyses. Analysis of contingency tables (Model I) for comparisons of scorpion size classes used the G-test of independence, and the comparison of scorpion height in vegetation used the analysis of variance (ANOVA) or the Kruskal-Wallis test when one of the assumptions of the ANOVA was not met (Sokal & Rohlf, 1981). Size classes I and II were pooled because of a zero for at least one class in the contingency tables. Planned comparisons were performed on a significant association ($P < 0.05$) for the contingency tables to test predictions on microhabitat preferences. For the monthly time periods, the data were pooled into three time periods based on a previous analysis of seasonal differences in microhabitat use (McReynolds, 2004). For the phases of the lunar cycle, planned comparisons were based on the amount of illumination with the first comparison being no moon present with the moon already set or not yet risen (waning crescent, waxing crescent after moon set and waning gibbous before moon rise), < 50% of the moon illuminated (waxing crescent before moon set) and > 50% of the moon illuminated (waxing gibbous and waning gibbous after moon rise); the second comparison between phases with no moon present (waning crescent vs. waxing crescent after moon set vs. waning gibbous before moon rise); and the third comparison between phases with > 50% of the moon illuminated (waxing gibbous and waning gibbous after moon rise). For the comparisons among microhabitats, the first planned comparison was between ground and vegetation. The second planned comparison was to test for differences among vegetation classes that were predicted to be used for foraging (*Acacia* spp.), for refuges (cacti) and other vegetation. The three-way G-test of independence was used to compare the microhabitat use by the different size classes of *C. vittatus* for either temperature or caterpillar availability classes (Sokal & Rohlf, 1981). Size classes I and II, all cacti, and various other microhabitat classes were pooled for the three-way contingency tables because of a zero in some classes. Conditional independence comparisons between microhabitat and size classes were not shown because of previous comparison in Fig. 3 and Table 1. The independence and total independence comparisons for the 3-way G-tests were not included because they provided no additional information. For the caterpillar availability table, blackbrush was a class and guajillo was pooled with other vegetation and not blackbrush because all trees sampled for caterpillar availability were blackbrush in this study.

Results

Microhabitat Use. The microhabitat use by the various size classes was significantly different (Fig. 3). In a planned comparison, there was no significant difference among size classes of scorpions on the ground versus climbing on vegetation (Table 1). In the planned comparison between vegetation classes, there was a significant association among size classes for scorpions on *Acacia* spp. vs. cacti vs. grass and other vegetation. In the planned comparison between the *Acacia* spp., there was no significant difference between blackbrush and guajillo. There were significant associations among size classes for scorpions on the cacti (tasajillo, prickly pear cactus and strawberry cactus) and on grass vs. other vegetation for these two planned comparisons (Table 1). A high frequency of size class IV was on prickly pear and strawberry cactus, but a low frequency of size class IV was on tasajillo (Fig. 3). A high frequency of size classes I and II were on grass, but a low frequency of size class I and II were on prickly pear cactus and very low frequency on strawberry cactus.

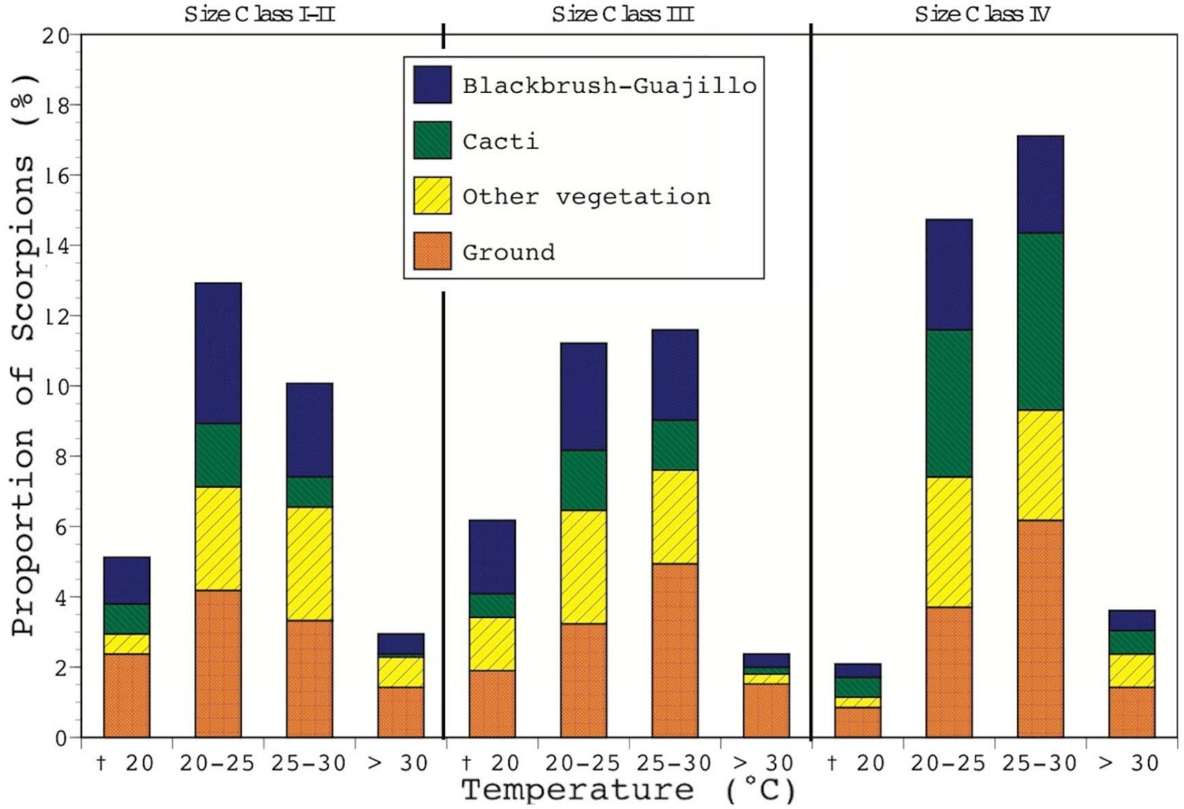

Figure 7: The proportion (%) of *C. vittatus* using different microhabitats among temperature and scorpion size classes (*n* = 1052). See Table 4 for a three-way G test of the contingency table among temperature, microhabitats and scorpion size classes.

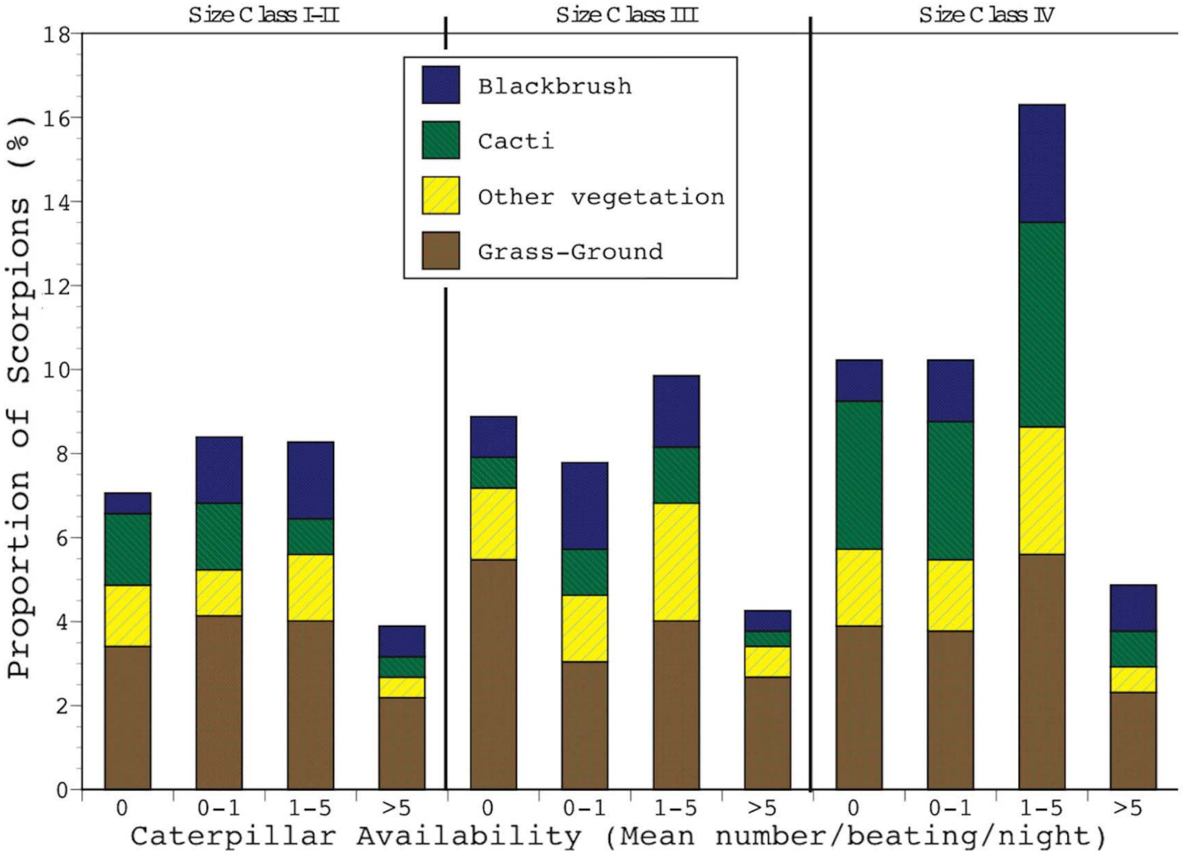

Figure 8: The proportion (%) of *C. vittatus* using different microhabitats among caterpillar availability and scorpion size classes (n = 822). See Table 5 for a three-way G test of the contingency table among caterpillar availability, microhabitats and scorpion size classes.

Comparisons	***G***	***df***	***P***
Interaction	20.530	18	ns
Conditional			
Temperature vs. Microhabitat	43.691	27	< 0.05
Ground vs. Vegetation	25.829	9	< 0.001
Blackbrush-Guajillo vs. Cacti + Other vegetation	3.215	9	ns
Cacti vs. Other vegetation	14.648	9	ns
Size vs. Temperature	64.335	24	< 0.001
≤ 25° C vs. > 25° C	27.904	8	< 0.01
≤ 20° C vs. 20-25° C	31.280	8	< 0.001
25-30° C vs. > 30° C	5.151	8	ns

Table 4: Three-way G test of independence of the contingency table for temperature vs. microhabitats vs. scorpion size classes. Planned comparisons were performed for conditional independence tests that were significant (P < 0.05). ns = not significant. See Fig. 7.

Comparisons	***G***	***df***	***P***
Interaction	13.720	18	ns
Conditional Independence			
Caterpillar availability vs. Microhabitat	36.026	27	ns
Size vs. Caterpillar availability	21.224	24	ns

Table 5: Three-way G test of independence of the contingency table for caterpillar availability vs. microhabitats vs. scorpion size classes. ns = not significant. See Fig. 8.

Height in Vegetation. A comparison of the mean height of scorpion among the size classes did not show a significant difference for most plant species and are not shown in this paper. The mean height of the size classes are shown for blackbrush and grass because the comparison in blackbrush demonstrates how high the different size classes can climb in vegetation and the one in grass is the only comparison that was significant (Fig. 4). The mean heights of scorpions on blackbrush were not significantly different using analysis of variance (ANOVA) with all size classes climbing in blackbrush having a mean height greater than 60 cm. The median heights in grass were significantly different among the size classes using a non-parametric test for the comparison because there were violations of the assumptions of ANOVA. The only two size classes that were significantly different in multiple comparison using a Tukey-Kramer unplanned comparison were size class III with the highest mean and median and size class I with the lowest mean and median (Fig. 4).

Monthly Activity. The activity of size classes with size classes I and II pooled had a significant association among time (months) classes (Fig. 5). In planned comparisons, the activity of the size classes was significantly different among three pooled time periods (January through April vs. May through August vs. September through December) (Table 2). The activity of the size classes had significant associations among months for January-February vs. March vs. April and May vs. June vs. July vs. August. However, the activity was not significantly different among September vs. October vs November-December (Table 2). The activity of size class I was low during all months except September and October. The activity of size class II was higher than the other size classes during January-February and November-December and had a low relative frequency during June and July. The activity of size class II increased and the activity of size class I decreased relative to the other size classes during November-December (Fig. 5). The pooling of size classes I and II is one probable reason that there was no significant difference in the planned comparison between September, October and November-December classes. The activity of size class III had the highest activity relative to the other size classes in March, April and June, and was the second most active in the other months except August. Size class IV had the lowest relative frequency during January-February and generally increased in relative frequency each month through September. The peak activity for size class IV relative to other size classes was during August, September and October (Fig. 5).

Figure 9: *Centruroides vittatus* on Texas prickly pear cactus (*O. engelmannii*) with grasshopper (Orthoptera) as prey.

Figure 10: *Centruroides vittatus* female on strawberry cactus (*E. enneacanthus*) with young on the dorsal prosoma and mesosoma.

Lunar Cycle. The activity of size classes was significantly different among phases of the lunar cycle (Fig. 6). In planned comparisons, the activity of size classes was not significantly different among classes pooled by the amount of illumination of the moon (Table 3). The lunar phases within the no moon class were significantly different among size classes with high frequency of size classes III and IV in the waning crescent phase relative to size classes I and II. The lunar phases within the > 50% illumination classes were marginally significantly different among size classes with higher frequency of size class IV relative to other size classes during waxing gibbous phase.

Microhabitat and Temperature. Scorpion activity among microhabitats, temperature and size classes was compared in a three way contingency table (Fig. 7). The three factor interaction comparison among microhabitats, temperature and size classes was not significant (Table 4). Both of the conditional independence comparisons were significant. The planned comparisons of the conditional independence of temperature versus microhabitat classes indicated that the significant association was ground versus vegetation (Table 4). The relative frequency of scorpions on the ground was higher when the temperature was > 30° C for all size classes but especially size class III (Fig. 7). A relatively high frequency of size class IV scorpions were on cacti at the intermediate temperatures (20-25° C and 25-30° C) (Fig. 7). The planned comparisons of the conditional independence of size class versus microhabitats indicated that the significant associations were ≤ 25° C versus > 25° C and ≤ 20° C versus 20-25° C (Table 4). Size classes I-II and III had a higher frequency than size class IV when temperatures were ≤ 25° C and size class IV was rarely active when temperatures were ≤ 20° C (Fig. 7). No scorpions were observed when the temperature was ≤ 10° C.

Microhabitat and Caterpillar Availability. Scorpion activity among microhabitats, caterpillar availability and size classes was compared in a three way contingency table (Fig. 8). The three factor interaction comparison among microhabitats, caterpillar availability and size classes was not significant (Table 5). Caterpillar availability did not have a significant association with either size class or microhabitat use by scorpions (Table 5). Neither microhabitat use by scorpions nor the activity of different size classes changed significantly with prey (caterpillar) availability.

Taxa of Prey Captured. A high proportion of scorpions observed for all size classes had no prey. No size class I scorpions were observed with prey during this period ($n = 85$). All other size classes (II, III and IV) captured caterpillars (Lepidoptera larvae), other insects that includes adult moths (Lepidoptera) and intraguild prey (IGP). The proportions of size class II scorpions with prey were caterpillars 1.4%, other insects 4% and IGP 1.1% ($n = 278$). The proportions (%) of size class III scorpions with prey were caterpillars 2.6%, other insects 3.9% and IGP 1.1% ($n = 381$). The proportions of size class IV scorpions with prey were caterpillars 1.7%, other insects 2.3% and IGP 1.7% ($n = 516$). There was no significant association among scorpion size classes (size classes I and II pooled) and different prey taxa or with no prey ($G = 7.702$, not significant, $df = 6$, $n = 1260$).

Discussion

The size classes of *C. vittatus* show microhabitat and temporal shifts in activity. The size classes of *C. vittatus* can shift activity because of three alternate hypotheses: (1) ontogenetic differences in foraging, (2) shifts due to risk from predators at different sizes or (3) direct interaction among size classes including cannibalism. Size class IV scorpions were on prickly pear (Fig. 9) and strawberry cactus (Fig. 10) at a higher frequency than the other size classes. *Centruroides vittatus* in south Texas prefer cacti (McReynolds, 2008). Either this preference for cacti is due to the preference by only size class IV scorpions perhaps as a diurnal refuge or the other size classes avoid cacti because of some risk when interacting with the larger scorpions. Cannibalism by *C. vittatus* (Fig. 11) has been observed in south Texas (McReynolds, 2008), but not at the rate observed in Arkansas (Yamashita, 2004). One possibility is that small scorpions can avoid the larger scorpions by avoiding the area around the preferred microhabitat of the larger scorpions on (or under) cacti.

Adult scorpions not using vegetation or juveniles using vegetation at a higher frequency than adults were observed by Polis (1980b) and Skutelsky (1996). Polis (1980b) hypothesized that *S. mesaensis* juveniles under (or in) vegetation were there to avoid cannibalism by the adults and Skutelsky (1996) hypothesized that *B. occitanus* juveniles avoided predators by climbing in vegetation. Juvenile *C. vittatus* in west Texas were climbing in vegetation at higher frequency than adults (Brown & O'Connell, 2000). Brown & O'Connell (2000) found more support for the predator avoidance hypothesis for climbing by C. *vittatus.* However, there is no support for smaller size classes of *C. vittatus* in south Texas climbing into vegetation to avoid larger size classes except perhaps size classes I and II using grass at a higher frequency. A higher proportion of scorpions of all size classes in south Texas were in vegetation (49% for size class I, 66% for II, 62% for III and 67% for IV) during this study compared to west Texas (19% in 1992 and 25% in 1993) (Brown & O'Connell, 2000) and Arkansas (1.6% of adults) (Yamashita, 2004). The size class IV scorpions were in all types of vegetation at high proportions relative to the other size classes except grass and tasajillo. Juvenile *C. vittatus* in south Texas cannot simply climb vegetation to avoid larger conspecifics as all size classes are frequently in vegetation and on the ground. There is no support for the hypothesis that smaller size classes climbed higher in vegetation to avoid the larger scorpions because the height of scorpions in different plants was not significantly different except for grass. In grass, a larger size class (III) climbed significantly higher than the smallest size class (I).

The alternate hypothesis for climbing by *C. vittatus* in west Texas was higher prey availability in vegetation than the ground (Brown & O'Connell, 2000). Climbing in vegetation such as blackbrush to forage for caterpillars (Fig. 12) is one possibility for *C. vittatus* in south Texas (McReynolds, 2004, 2008). However, there is no support for shift in activity by the different size classes to climb in blackbrush to forage for caterpillars. There was no observable difference in the use of blackbrush and guajillo by the different size classes, and the mean height of the scorpion in blackbrush was not significantly different among size classes. In addition, the type and frequency of prey captured was not significantly different among the size classes. Therefore, all

Figure 11: *Centruroides vittatus* cannibalism with size class IV scorpion feeding on size class III on tasajillo (*O. leptocaulis*).

size classes can apparently climb in blackbrush to forage for caterpillars and perhaps climb in other vegetation to forage and feed as well.

All size classes were observed during all three periods and most months. This high overlap in temporal activity between size classes can be due to long periods of growth for instars, asynchronous growth of different instars, long life of adults, asynchronous and/or long breeding seasons (see Wissering, 1988). Courtship of *C. vittatus* has been observed from May to October and females carrying young were observed mainly in July and August but in September and as late as October and as early as May from 2000 to 2010 at this study site (unpbl. data). The frequency of size class I began to increase in July and August and was highest in September and October because second instars could be dispersing from the female's dorsal mesosoma after their first molt during these months.

In *Smeringurus mesaensis*, the younger age classes are active during cooler periods when adults are rarely active (Polis, 1980a, 1984). Neither juvenile *C. vittatus* in west Texas nor juveniles and second instar *C. vittatus* in Arkansas show a shift in activity to cooler periods to avoid adults (Brown & O'Connell, 2000; Yamashita, 2004). The activity of smaller scorpions does extend into November-December and January-February because of the mild winter in south Texas. However, there does not appear to be a temporal refuge for the smaller scorpions because size class IV has high relative activity during all months except during January-February when the overall activity is low. The activity of size class II does decrease during April through July. This could be due to a molt to size class III, but it also could be due a reduction in activity when larger size classes are active.

Hadley & Williams (1968) predicted that the activity of scorpions will decrease with increase in lunar illumination. This change in activity during the lunar cycle is perhaps because of nocturnal visual predators (Warburg & Polis, 1990). Adult scorpions but not juveniles reduced activity during high illumination of the lunar cycle for *Buthus occitanus* (Skutelsky, 1996) and *Mesobuthus gibbosus* (Brullé, 1832) (Kaltsas & Mylonas, 2010). However, not all scorpions differ in activity because of the lunar cycle including *Centruroides sculpturatus* Ewing, 1928 (Hadley & Williams, 1968) and *S. mesaensis* (Polis, 1980a). A possible temporal refuge for one or more of the *C. vittatus* size classes can be during the lunar cycle, if the activity of a size classes depends on the size class's vulnerability to predators at different lunar illuminations. The size classes did differ among lunar cycle phases but not because of differences in illumination during the lunar cycle (no moon vs. ≤ 50% vs. > 50% of the moon illuminated). Instead size class IV was more active during the waxing gibbous than during waning gibbous after moon rise. This is counter to the activity of adult *Buthus occitanus* (Skutelsky, 1996) perhaps because large *C. vittatus* are less vulnerable to predation by visual predators. In addition, size classes III and IV had higher relative activity during waning crescent than during waning gibbous before moon rise or waxing crescent after moon set. There are no explanations proposed for these differences in activity among the classes with no moon.

Two important factors that influence the activity of age classes in *S. mesaensis* are temperature and prey availability (Polis, 1980a, 1984; Polis & McCormick, 1986). For *C. vittatus* in this study, temperature is important in determining the activity of size classes in different microhabitats but not prey (caterpillar) availability. The activity of size class IV is low when temperatures are ≤ 20° C and the activity of size classes I and II (pooled) and III is higher than size class IV. This fits the hypothesis that smaller scorpions will be active during sub-optimal conditions to avoid interactions with the larger scorpions (Polis, 1980a, 1984; Polis & McCormick, 1986). However, all size classes have high activity at higher temperature classes either because nights with temperatures ≤ 20° C in south Texas are rare and/or the smaller size classes are still active at higher temperatures even though they can encounter the larger size classes. The adult females of *Paruroctonus utahensis* reduce activity with lower temperatures and shortly afterwards the juveniles become inactive that night because the temperature has dropped too low for juveniles, and thus juveniles are usually active at the same time as the adult females (Bradley, 1988). For *C. vittatus*, small scorpions can increase activity within a temperature range where size class IV scorpions were inactive and before no scorpions were active (≤ 10° C). At higher temperatures (> 30° C), relatively more scorpions were on the ground. This fits the pattern observed in previous studies of *C. vittatus* with a high frequency of scorpions on the ground during summer months of July and August and at high temperatures (McReynolds, 2004, 2008). Carlson & Rowe (2009) found that *C. vittatus* have a higher metabolic rate at higher temperatures and faster running speed and proposes that scorpions on the ground then have a high probability of escaping predation. The highest proportion of size class IV scorpions on cactus was during intermediate temperatures. This does not support the hypotheses that cacti are used as a refuge during high and low temperatures but does not disprove the hypothesis either because the hypothesis is that cactus is a refuge from high diurnal temperatures (see McReynolds, 2008). The temperatures measured in this study are not a test of the hypothesis because nocturnal temperatures can drop below 30° C even when diurnal temperatures are high.

In *Smeringurus mesaensis*, adult scorpion activity has a direct correlation with prey abundance, but juv-

Figure 12: *Centruroides vittatus* on blackbrush (*A. rigidula*) with caterpillar as prey.

enile scorpion activity had an inverse correlation with prey abundance (Polis, 1980a; Polis & McCormick, 1986). Juvenile *S. mesaensis* can be avoiding the adults by being active during lower quality foraging times (Polis, 1980a; Polis & McCormick, 1986). In south Texas, there was no significant shift in the use of blackbrush by size classes of *C. vittatus*. In addition, the capture of caterpillars and other prey among the size classes of *C. vittatus* was not significantly different, and there was no increase in activity on blackbrush when caterpillar availability increased in blackbrush. Therefore, there was no support for ontogenetic shifts to blackbrush because of prey (caterpillar) availability. Two factors that can influence caterpillar availability were not considered in this study. First, there could be a time lag in scorpion activity in response to caterpillar availability, and second, scorpion activity on trees could reduce caterpillar availability either directly by predation on caterpillars or indirectly by caterpillars escaping from trees when scorpions move on the trees (see Power, 1992; Rudolf, 2007). Only caterpillar availability was considered and availability of other prey could influence foraging behavior. Differences in foraging activity and microhabitat use by the size classes because of availability of other prey are possible. For example, smaller size classes foraging more in grass for small prey such as termites is a possible explanation for the high frequency of size classes I and II in grass.

The results show that size classes of *C. vittatus* have significant microhabitat and temporal shifts. Nevertheless, there is no evidence that size classes have shifts in foraging nor does the activity during lunar cycle fit the predicted pattern if visual predators are affecting activity. The activity of the smaller size classes still has large temporal overlaps with size class IV thus avoidance of large scorpions by temporal shifts is not supported. The observation that size class IV scorpions frequently using prickly pear or strawberry cactus and the smaller size classes rarely use either cactus suggests the most promising direction for further research. Risk of intraguild predation by *S. mesaensis* could reduce activity of other scorpion species in a preferred habitat (sand substrate) (Polis & McCormick, 1986, 1987). In a similar manner, smaller *C. vittatus* could possibly be avoiding larger scorpions and possible cannibalism by avoiding the preferred microhabitat (prickly pear and strawberry cactus) of large scorpions. Further study is needed to distinguish between this hypothesis and other alternate hypotheses of different microhabitat preferences among scorpion size classes or shifts due to risk from predators at different sizes.

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