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The effect of microhabitat use on the foraging and diet of the striped bark scorpion, *Centruroides vittatus* (Buthidae: Scorpiones) in blackbrush habitat of south Texas

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Abstract. Microhabitat use by predators can be influenced by prey availability, predator size and risk of cannibalism. The preferred microhabitat for a predator can be for foraging, feeding or as a refuge. In this study in south Texas, *Centruroides vittatus* (Say, 1821) of all size classes utilized both ground and vegetation microhabitats. There was a high proportion of scorpions with caterpillars in legumes and low proportion of scorpions with any of the prey types on the ground. The median height of scorpions with prey did vary, with scorpions on legumes with caterpillar prey the highest and scorpions on other vegetation with dangerous prey the lowest. Intermediate size scorpions used legumes at a high frequency during January–April, and large scorpions used succulents at very high frequency during September–December. Scorpions climbed higher in blackbrush and other legumes than in other vegetation types. These results suggest that scorpions are actively foraging for caterpillars in legumes, and legumes are a quality microhabitat for foraging. The low proportion of scorpions with prey on the ground suggests that *C. vittatus* feed on prey on vegetation even if the prey was captured on the ground. A possible advantage for the scorpion to handle and consume prey on vegetation is lower predation risk or interference while feeding. The high use of succulents by the large scorpions cannot be explained by foraging success. A possibility is that succulents are preferred refuges by all *C. vittatus* but smaller scorpions avoid succulents because of the risk of cannibalism by the larger scorpions.

Keywords: Quality microhabitat, scorpion size, scorpion height, scorpion diet, caterpillar prey

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Habitat and microhabitat can determine foraging success because of differences in prey availability (Griffiths 1975; Werner et al. 1981) or foraging efficiency (Hill et al. 2004). Habitat selection at one temporal or spatial scale can be based on prey availability but at another scale based on refuges (Orians & Wittenberger 1991). The habitat and microhabitat used for foraging are determining feeding rate by affecting prey availability, access to prey—including access to different types of prey—and cost to capture prey (Warfe & Barmuta 2004). Microhabitat use can shift with seasonal changes because of changes in prey availability (Vonshak et al. 2009). Activity can change with seasonal increases in prey availability, but at spatial and short-term scale, differences in prey availability at the local level (microhabitat) are not always predictable and the predator might not be able to track the fluctuations (Bradley 1993)

Foraging by many predators, including scorpions, can involve two different methods: active search or ambush (sit-and-wait); the search method can determine feeding rate, including type of prey captured, because of differences in the prey encountered (Inoue & Matsura 1983). The habitat and microhabitat used can affect effectiveness of foraging method or what foraging method is used if the predator switches between active search and ambush (Werner et al. 1981; Werner & Hall 1988; Ehlinger 1990; Skutelsky 1995; Halaj et al. 1998; Delclos & Rudolf 2011). In addition, habitat and microhabitat use can determine risk of interference from other foragers or risk of predation, including intraguild predators and cannibals (Polis & McCormick 1987; Polis 1988a; Rudolf 2006, 2007, 2008; Rudolf & Armstrong 2008). A predator can use a different habitat or microhabitat to reduce risk of interference or predation, but this tradeoff to reduce risk of interference or predation can reduce foraging success (Hossie & Murray 2016).

The size and age of predator can determine foraging success by affecting type and effectiveness of foraging method and diet (Smith & Petranka 1987; Cisneros & Rosenheim 1997) and risk of interference competition from other predators (Geraldi 2015) or risk of cannibalism and intraguild predation by larger predators on smaller predators (Murdoch & Sih 1978; Sih 1981, 1982). The response to risk of interference or predation can be a temporal or habitat shift (Polis 1988a; Rudolf 2007; Rudolf & Armstrong 2008). The predator most vulnerable to cannibalism can shift habitat or temporal activity (Murdoch & Sih 1978; Sih 1981, 1982; Polis 1980a, 1984) to avoid predation (Mittelbach 1984; Werner & Hall 1988). Larger or older individuals can exclude smaller or younger individuals from the habitat with lower risk of predation (Cresswell 1994). These shifts in habitats 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 1987).

The low metabolic rate of scorpions can explain the high biomass and abundance of scorpions in arid environments, and high abundance of scorpions can contribute to juvenile scorpions being an important prey item for adults and larger juvenile scorpions (Lighton et al. 2001). Scorpion size (and age) can also influence activity and microhabitat. For example, in the sand scorpion, *Smeringurus mesaensis* (Stahnke, 1957) (formerly *Paruroctonus mesaensis*), age influence surface activity over time (Polis 1980a), foraging (Polis 1984, 1988b), cannibalism (Polis 1980b), intraguild predation (Polis & McCormick 1987) and home range (Polis et al. 1985).

Two environmental factors influence activity of scorpions of different ages: temperature (Polis 1980a) and prey abundance

(Polis 1980a, 1988b). Scorpions of different size or age can utilize different habitats or microhabitats, with adults using the optimal habitat (sand dunes) and juveniles and heterospecific scorpions in sub-optimal habitats (heterogeneous and hard pan) because of intraguild predation (Polis & McCormick 1987), with juveniles foraging on vegetation at higher frequency than adults (Bradley 1988; Skutelsky 1996). Seasonal shifts in activity of juvenile and adult scorpions can occur (McReynolds 2004, 2012; Araujo et al. 2010), but a temporal shift between juveniles and adult females does not occur for all scorpions (Bradley 1988).

In earlier studies *Centruroides vittatus* (Say, 1821) (Scorpiones; Buthidae) in west Texas, juveniles were found to climb more than adults on vegetation and climb higher (Brown & O'Connell 2000), and temporal differences in surface activity occur in adults and juveniles with ontogenetic shifts in the activity of *C. vittatus* (see McReynolds 2012, 2020). Caterpillars are important prey items for *C. vittatus* in South Texas, and scorpions are often observed feeding on caterpillars in blackbrush (McReynolds 2008). Microhabitat use by *C. vittatus* shows a preference for cacti (McReynolds 2008), and a higher proportion of large scorpions relative to small scorpions are observed on cacti (McReynolds 2012). Brown & O'Connell (2000) hypothesize that *C. vittatus* climb vegetation either to reduce risk of predation or to forage on vegetation. Additional hypotheses for why *C. vittatus* climbs on vegetation include errant scorpions using vegetation as a diurnal refuge (McReynolds 2008, 2012) and scorpions feeding on prey while on vegetation (see Brown & O'Connell 2000).

Comparisons among *C. vittatus* were performed on microhabitat use, taxa of prey in the diet, height of the scorpion on vegetation, and seasonal activity, to determine the quality of different microhabitat(s) for scorpion foraging, feeding and/or refuge. The microhabitat quality hypothesis for foraging predicts the following: (1) A high-quality microhabitat is the preferred foraging site for all scorpions because of high foraging success, and the preferred prey for scorpions of all sizes scorpions has high availability in this microhabitat. (2) Smaller scorpions would be at risk of cannibalism in the high-quality microhabitat, and thus shift to sub-optimal microhabitats, thereby reducing their access to preferred prey. Results of the first comparison in this study suggest a possible high-quality microhabitat for foraging based on foraging success (feeding rate). Another comparison compares microhabitat use by different size scorpions and at different seasons to test if the possible high-quality microhabitat fits the predictions of the hypothesis for foraging and to determine if there is any evidence for a preferred microhabitat for feeding or as a refuge. If a microhabitat is used for foraging on vegetation, it is expected that scorpions will climb high into vegetation to search for prey, especially caterpillars, and remain high in the vegetation to feed. Comparisons of the height in vegetation of scorpions with prey and without prey will determine if there is a difference in vegetation use for foraging and feeding.

METHODS

Study animal.—*Centruroides vittatus* (Scorpiones, Buthidae) has a wide distribution with Laredo, Texas in the southern portion of the distribution (Shelley & Sissom 1995). *Centruroides vittatus* is nocturnal, with refuges in debris, beneath vegetation, under bark, and in holes in the ground used during the day, but *C. vittatus* and other bark scorpions rarely dig their own burrows (Polis 1990) and were not observed digging a burrow during this study. 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 of *C. vittatus* between April and September and age of maturity between 36 and 48 months (Polis & Sissom 1990). On nights of emergence, *C. vittatus* was active on the ground and/or on vegetation. Both courtship and females carrying first instars were occasionally observed in the field (pers. obs.). Voucher specimens of *C. vittatus* were deposited in the invertebrate collection at Texas A&M International University.

Size classes.—*C. vittatus* observed in the field were placed in one of four size classes by the observer; the scorpions were not collected or directly measured in the field. This is similar to the method used to estimate age classes for *S. mesaensis* (Polis 1980a, 1984; Polis et al. 1985). Size classes of *C. vittatus* were based on estimates of the length of the scorpion from the anterior of the prosoma to the posterior of the mesosoma (see McReynolds 2012). This measure of scorpion size was used in a study of *S. mesaensis* (Polis & McCormick 1987). Scorpion size classes were: Size class I $<$ 5 mm, Size class II between 5–10 mm, Size class III between 10–15 mm and Size class IV $>$ 15 mm (see McElroy et al. 2017). Size class IV scorpions included adult males and females, but some penultimate instars were included in the size class. Size class I scorpions included second instars after molting from first instars that are on the dorsal mesosoma of the female scorpion (Polis & Sissom 1990). However, size classes do not correspond to instars or age classes for *C. vittatus* in this study. An association between size and age is not possible at this time for *C. vittatus* in south Texas because its life history has not been determined for south Texas and the birth period is not discrete (see Polis 1984). The estimate of age to maturity is 36 to 48 months (Polis & Sissom 1990), but this cannot be associated with size estimates.

Habitat.—This study was done on the campus of Texas A&M International University (27° 35′ N, 99° 26′ W), Laredo, Texas. Laredo is in the Tamaulipan Biotic Province, characterized by low precipitation and high average temperatures (Blair 1950). The habitat of the research plots can be described as thorny brush (Blair 1950) or chaparral. Vegetation in the plots included legumes such as blackbrush acacia (*Vachellia rigidula* formerly *Acacia rigidula*), guajillo (*Senegalia berlandieri* formerly *Acacia berlandieri*) and honey mesquite (*Prosopis glandulosa*); succulents such as Texas prickly pear cactus (*Opuntia engelmannii*), tasajillo (*Cylindropuntia leptocaulis*), strawberry cactus (*Echinocereus enneacanthus*) and Spanish dagger (*Yucca treculeana*), and other plant species such as cenizo (*Leucophyllum frutescens*), guayacan (*Guaiacum angustifolium*), leather stem (*Jatropha dioica*), lotebush (*Ziziphus obtusifolia*) and other plant species.

Data collection.—Scorpions were observed at night by locating the scorpion fluorescing under ultraviolet light (see Sissom et al. 1990). 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 scorpions for this comparison were collected

from August 27, 2003 to November 11, 2013. 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. Data were collected on all scorpions observed within the study site, approximately 50 hectares in area. Data collected for each scorpion included date and time of observation, species of scorpion, size class of scorpion (see above), microhabitat used, height of the scorpion above the ground (if on vegetation), whether the scorpion had prey or not, and prey taxa to order. The height of the scorpion was measured with metric tape in centimeters from the ground to the location of the scorpion in the vegetation. All months of the year were sampled (9 nights in January, 59 nights in February, 70 nights in March, 75 nights in April, 39 nights in May, 55 nights in June, 62 nights in July, 41 nights in August, 90 nights in September, 95 nights in October, 43 nights in November and only 2 nights in December), but scorpions were rarely active during December and January. Scorpions can be active during all other months, especially when night time temperatures are above 20° C (see McReynolds 2008).

For use in contingency tables the microhabitat data were pooled into five classes: ground, grass, legumes, succulents, 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. Legumes included blackbrush, guajillo and mesquite. Legumes were placed into two classes, blackbrush and other legumes, for comparisons of height of scorpion above the ground on vegetation. Succulents included prickly pear cactus, tasajillo, strawberry cactus and *Yucca*. Other vegetation included perennial shrubs such as cenizo, guayacan, leather stem and lotebush, and small trees that are rarely taller than 2 meters. Annuals were rare in the habitat except for ephemeral wildflowers after heavy rains, and scorpions were rarely observed climbing these wildflowers. Prey capture classes included no prey captured, caterpillars (Lepidoptera larvae), orthopterans, moths (adult Lepidoptera), intraguild prey (IG prey) including Scorpiones, Araneae, Solifugae, Opiliones, Mantodea and Chilopoda, and other prey. Prey capture by scorpions can be observed as scorpions digest externally; thus, prey items can be observed in pedipalps or chelicerae (Polis 1979). Feeding rate as an indication of foraging success is the number of scorpions with prey per total number of scorpions observed for each class. This is the same as feeding rate for *S. mesaensis* (Polis 1979; McCormick & Polis 1990).

Data analyses.—Contingency tables were analyzed using the two-way G-test of independence to compare prey capture versus microhabitat and three-way G-test of independence to compare scorpion size classes, months of the year and microhabitat (Sokal & Rohlf 2012). The data were pooled because the G-test cannot be performed when a value in the table is zero. The months of the year were pooled because December had zero scorpions observed and no scorpions with prey in January and February. Orthogonal planned comparisons were performed for both G-tests (Sokal & Rohlf 2012). The height above ground of scorpions on different vegetation types with different prey types were compared. For the comparison of prey types, intraguild prey and orthopteran prey were pooled as dangerous prey and moths and other prey were pooled as other prey. Dangerous prey are those that can be difficult to capture and perhaps even injure the scorpion as the prey attempts to escape (by delivering venomous sting or bite or a powerful kick). In addition, the height of scorpions on different vegetation types and with different prey types were compared. The non-parametric Kruskal-Wallis test was performed for both comparisons of scorpion height above ground instead of the Analysis of Variance (ANOVA) test because some assumptions of the ANOVA such as equal standard deviations between classes and normality for all classes were not meet (Sokal & Rohlf 2012). An unplanned comparison using Dunn's multiple comparisons was performed when the Kruskal-Wallis test was significant (Sokal & Rohlf 2012).

RESULTS

Microhabitat and prey type.—*Centruroides vittatus* used the ground (35.8%) more than any other microhabitat, followed by legumes (including blackbrush), then succulents, other vegetation, and grass the least used (Fig. 1). The prey types of *C. vittatus* were significantly different among microhabitats (Fig. 1, $G = 301.522$, $df =$ degrees of freedom $= 20$, $P < 0.001$). Orthogonal planned comparisons were performed on the contingency table from the data in Fig. 1. The frequency of scorpions with prey (all five classes of prey) on the ground was significantly lower compared to scorpions on vegetation (Ground versus All vegetation: $G = 219.823$, $df = 5$, $P < 0.001$). The frequency of prey types for scorpions on legumes (including blackbrush) was significantly different from other microhabitats, including grass, succulents and other vegetation (Planned comparison: Legumes versus All other vegetation: $G = 73.220$, $df = 5$, $P < 0.001$). A high proportion of scorpions with caterpillar prey was found on legumes. The frequencies of prey types were not significantly different among grass, succulents and other vegetation (Grass versus Succulents versus Other vegetation, $G = 8.479$, $df = 10$, not significant). For *C. vittatus*, the proportion of scorpions on vegetation with caterpillar prey was 99.2% (n = 123) and on vegetation with other prey was 96.7% (n = 181). In contrast, there were only 62.8% (n = 7147) of *C. vittatus* with no prey on vegetation. The median heights above ground of scorpions on different vegetation types (legumes vs. other vegetation), and among scorpions with caterpillar, dangerous and other prey, were significantly different (Fig. 2). The average heights of scorpions on legumes with caterpillar or other prey were high while the scorpions with dangerous prey were intermediate (Fig. 2). The average heights of scorpions on other vegetation with caterpillar or other prey were intermediate while the scorpions with dangerous prey were low. In unplanned comparisons, scorpions on legumes with caterpillar or other prey were significantly higher than scorpions on other vegetation with caterpillar, dangerous or other prey. Scorpions on other vegetation with dangerous prey were significantly lower than scorpions on legumes with caterpillar, dangerous or other prey (Fig. 2).

Microhabitat use and scorpion size.—Scorpion size classes versus microhabitats versus months of the year were compared for all scorpions (with or without prey) in a contingency table using data presented in Fig. 3. The interaction comparison for

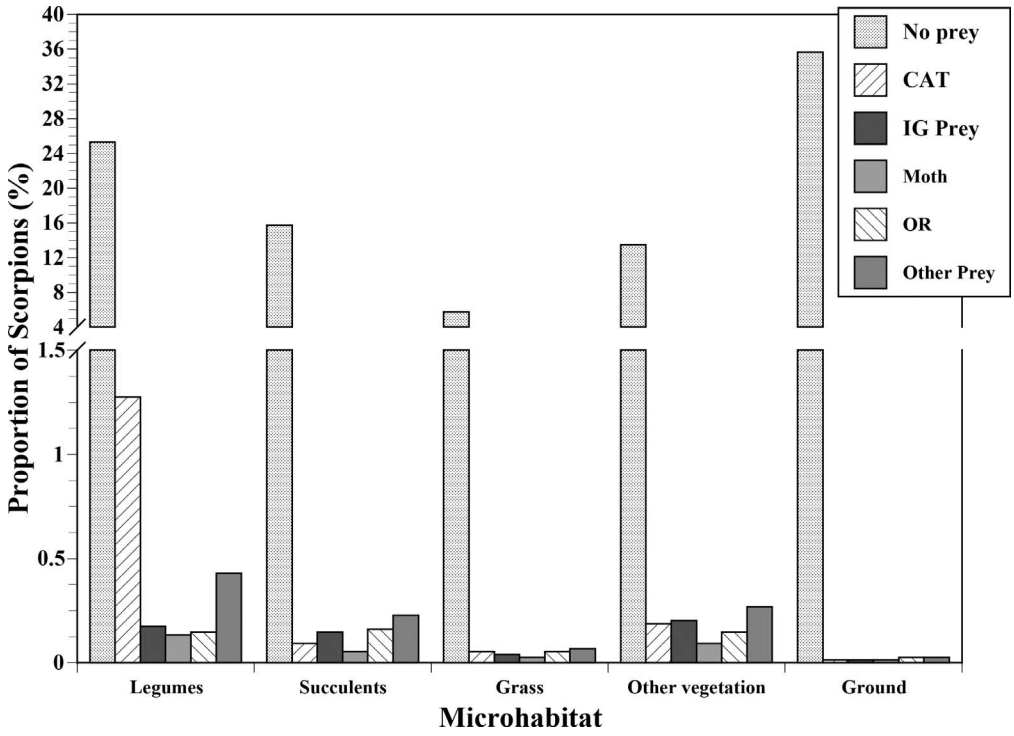

Figure 1.—The proportion (%) of *C. vittatus* with different prey types including scorpions with no prey, caterpillar (CAT), intraguild (IG Prey), moth, orthopteran (OR) and other prey among different microhabitats. The frequency of scorpions with different prey types was significantly different among microhabitats ($G = 301.522$, $P < 0.001$, $df = 20$, $n = 7451$). See text for planned comparisons among prey types.

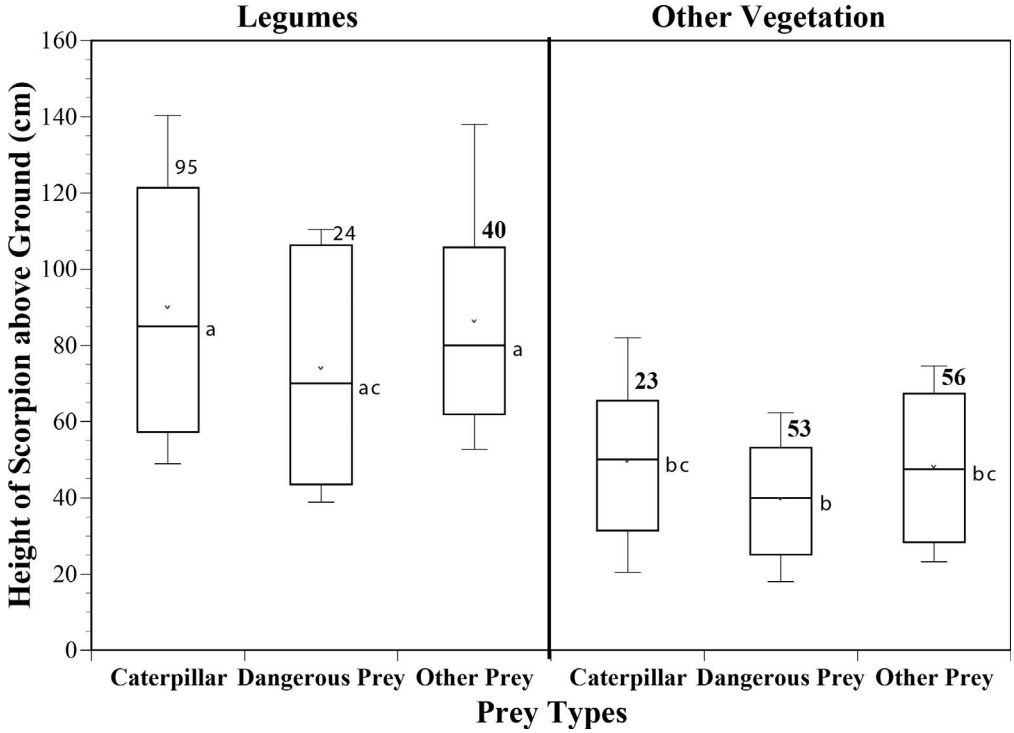

Figure 2.—The median height above ground of *C. vittatus* scorpions with caterpillar or other prey, on either legumes (including blackbrush) or other vegetation. The boxplots show the median and upper and lower quartiles, and whiskers show standard deviations from the means (± 1 SD). Sample sizes (n) are above the boxplot. Median scorpion height was significantly different among prey types (Kruskal-Wallis Statistic: $H = 78.0$ (corrected for ties), $P < 0.001$). Medians with the same letter next to the boxplot were not significantly different in unplanned comparisons using Dunn's Multiple Comparisons Test.

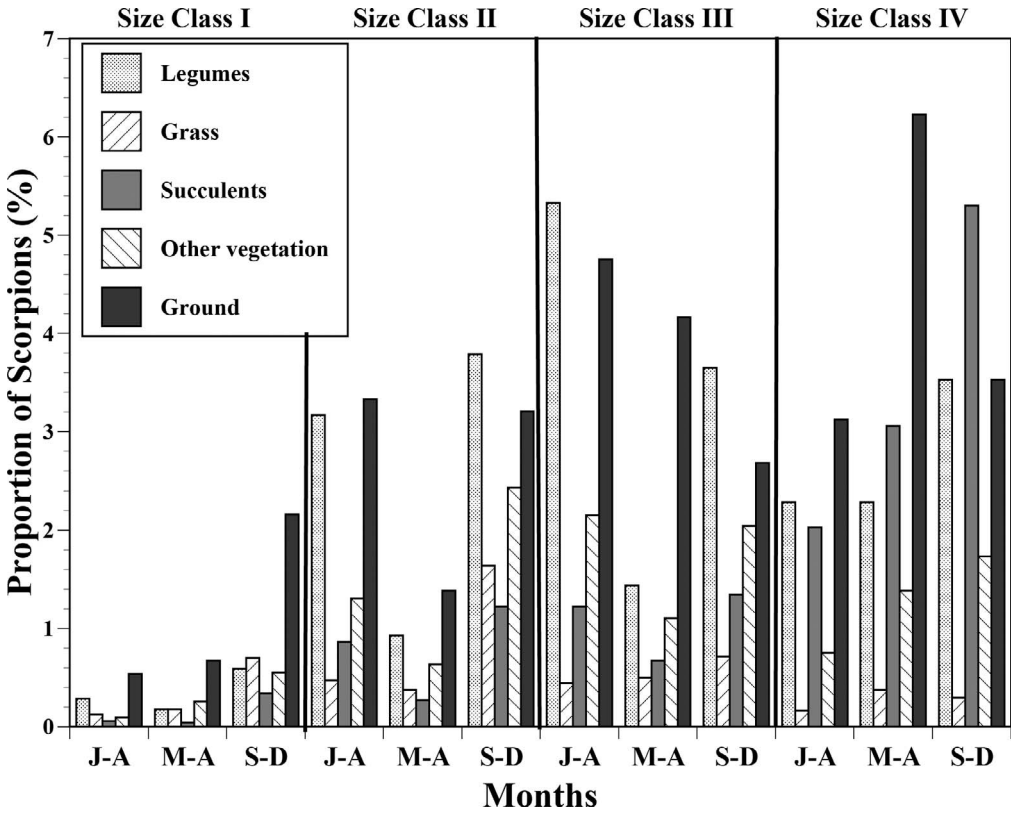

Figure 3.—The proportion (%) of *C. vittatus* with and without prey using different microhabitats among months of the years and scorpion size classes ($n = 7449$). Three-way G test interaction comparison was significantly different ($G = 51.430$, $df = 24$, $P < 0.001$) Months of the year were pooled with J-A = January through April, M-A = May through August and S-D = September through December. Interaction, conditional and orthogonal planned comparisons of a three-way G test of the contingency table among microhabitats, months of the year and scorpion size classes were performed but not shown. See Table 1.

the three-way G test of independence for microhabitats versus months of the year versus scorpion size classes was significant ($G = 51.430$, $df = 24$, $P < 0.001$). All three conditional tests comparing months of the year, microhabitats and scorpion size classes were significant, as would be expected when an interaction test was significant. All orthogonal planned comparisons of microhabitats for conditional tests were significant (Table 1). Three possible reasons for the high interaction effect were high activity of size class III and IV scorpions on the ground during May–August, high activity of size class III scorpions on legumes during January–April and high activity of size class IV scorpions on succulents during September–December (Fig. 3). The highest activity for size class I scorpions was during September–December, and the highest proportion on the ground for all three time periods were size class I scorpions. The proportion of size class III and IV scorpions on the ground was high relative to vegetation use during May–August (Fig. 3). Size class III scorpions had the highest activity on legumes (especially blackbrush) during January–April for any size class or months of the year and had high activity on legumes during September–December. Size class IV scorpions had the highest activity of any size class on succulents especially in September–December but was rarely on grass. Size class II scorpions had the highest proportion on grass during September–December of any size class (Fig. 3).

The median heights of scorpions with no prey among vegetation types were significantly different (Fig. 4). Average height of scorpions on grass were the lowest then succulents, other vegetation, other legumes, and finally scorpions on blackbrush the highest (Fig. 4). In unplanned comparisons, the average heights of scorpions on the different vegetation types were all significantly different from one another (Fig. 4).

DISCUSSION

The microhabitat use by scorpions was influenced by the scorpion size and the season, and microhabitat use influenced foraging success. Reasons for scorpions to climb vegetation are to either to reduce risk of predation, forage or feed (see Brown & O'Connell 2000) or use vegetation as a diurnal refuge (McReynolds 2008, 2012). For *C. vittatus* in blackbrush habitat in south Texas, ground was utilized more than any other microhabitat with legumes and especially blackbrush next. However, all size classes of scorpions were observed climbing into various vegetation types for a higher proportion of scorpions on vegetation than on the ground. Therefore, it is important to determine how scorpions are using vegetation versus how they use the ground. Scorpions can use the ground for many of the same reasons as use of vegetation such as foraging for prey or feeding. In addition, scorpions can transition from one plant to another plant on the ground or move from a refuge on the ground (hole or rodent or wolf

Table 1.—Three-way G test of independence of the contingency table for microhabitats versus months of the year versus scorpion size classes. See Figure 3.

Comparisons	*G*	*df*	*P*
Interaction	51.430	24	< 0.001
Conditional			
Months of the Year versus Microhabitat	366.984	32	< 0.001
Planned Comparisons			
Ground versus Vegetation	247.897	8	<0.001
Legumes versus Succulents, Grass and Other vegetation	78.911	8	< 0.001
Succulents versus Grass and Other vegetation	18.921	8	< 0.05
Grass versus Other vegetation	21.256	8	< 0.001
Size Class versus Microhabitat	755.069	36	< 0.001
Planned Comparisons			
Ground versus Vegetation	103.028	9	< 0.001
Legumes versus Succulents, Grass and Other vegetation	72.535	9	< 0.001
Succulents versus Grass and Other vegetation	497.905	9	< 0.001
Grass versus Other vegetation	81.601	9	< 0.001
Size Class versus Months of the Year	624.190	30	< 0.001

spider burrow) to vegetation and back. For *C. vittatus*, these uses of microhabitat are not mutually exclusive with scorpions performing many of these activities during one night. *Centruroides vittatus* uses a variety of plant species and the ground for various reasons.

Activity in different microhabitats.—Scorpions can utilize different habitats and microhabitats based on soil type (Bradley & Brody 1984) or vegetation (McReynolds 2004, 2008, 2012; Piñero et al. 2013). Scorpions including *S. mesaensis* (Polis 1979, 1988b), *C. vittatus* in west Texas (Brown et al. 2002) and south Texas (McReynolds 2004, 2008, 2012, 2020) and *Microtityus jaumei* Armas, 1974 in Cuba (Cala-Riquelme & Colombo 2011) show seasonal differences in activity and prey capture rates. An important conclusion

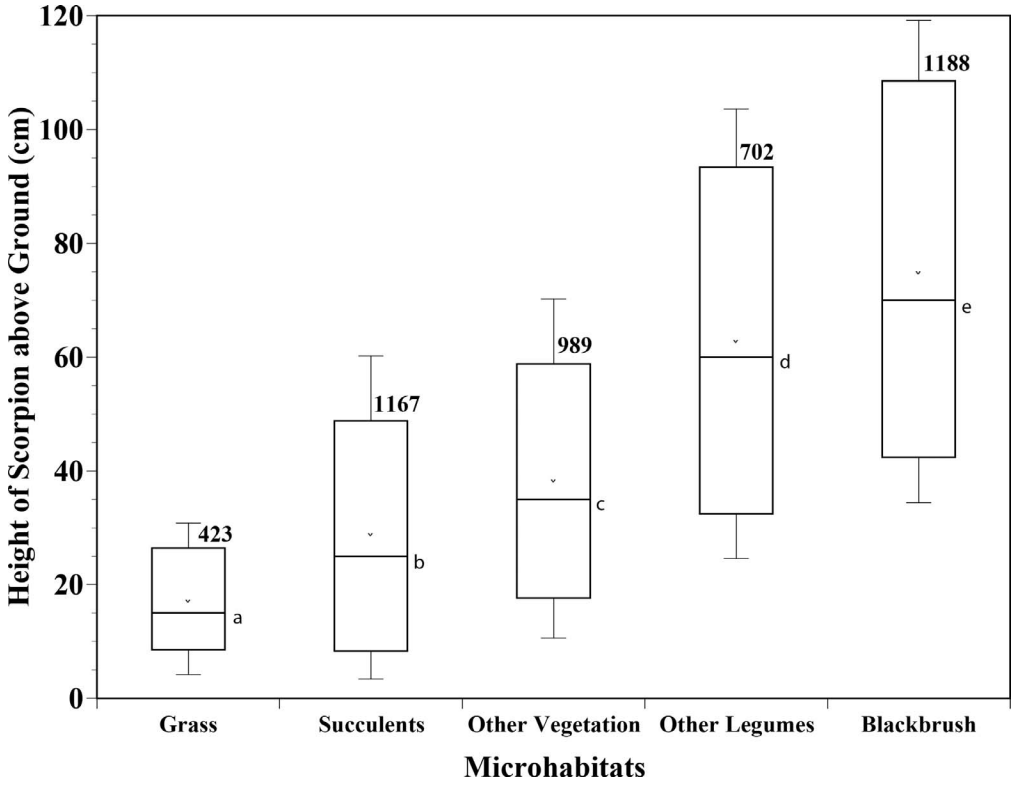

Figure 4.—The median height of *C. vittatus* above ground with no prey on either grass, succulents, other vegetation, other legumes or blackbrush. The boxplots show the median and upper and lower quartiles and whiskers show standard deviations from the means (± 1 SD). Sample sizes (*n*) are above the boxplot. Median scorpion height was significantly different among vegetation types (Kruskal-Wallis Statistic: H = 1357.9 (corrected for ties), $P < 0.001$). Medians with the same letter next to the boxplot were not significantly different in unplanned comparisons using Dunn's Multiple Comparisons Test.

from this study is that all size classes of scorpions climb on vegetation and not just to feed. All *C. vittatus* in west Texas do climb into vegetation (Brown & O'Connell 2000) but not at as high of frequency as in south Texas. The proportion of *C. vittatus* on vegetation instead of the ground or other substrates in west Texas is between 19.3-25.2% (Brown & O'Connell 2000) and in Arkansas 3.7% (Yamashita 2004) while in south Texas a much higher proportion of *C. vittatus* were on vegetation. That both adults and juveniles climb into vegetation is not what has been observed for other scorpion species, in which climbing by juveniles occurs more often and climbing by adults is rare (Bradley 1988; Skutelsky 1996). Microhabitat use varied with both season and size class of *C. vittatus*. Differences in locomotor ability among adults and juveniles and males and females (see Carlson et al. 2014) could explain some differences in frequency of climbing seen during different time periods and differences in what vegetation is climbed by different size classes (e.g., juveniles in grass). Nevertheless, all size classes of scorpions climb and all utilize the ground. Therefore, much of the variation in microhabitat use by different size scorpions during different seasons is mainly due to microhabitats having various functions.

Foraging on vegetation.—For *C. vittatus*, a major implication of this study is that scorpions climb into blackbrush and other legumes to forage, and the major prey of these scorpions in blackbrush and other legumes is caterpillars. While this is true of all size classes, it is intermediate-size scorpions that capture more caterpillars (McReynolds 2020). Most caterpillar prey for *C. vittatus* in south Texas were consumed in blackbrush and other legumes where caterpillar availability can be high but varies temporally in blackbrush with precipitation levels (Quintanilla 2008). The median heights of scorpions with caterpillar prey on legumes are higher than scorpions with caterpillar, dangerous or other prey on other vegetation. In addition, scorpions climb higher in blackbrush then other legumes, other vegetation, succulents and grass the lowest. *Centruroides vittatus* climbing higher in legumes to actively forage for caterpillars and other prey can explain these results. Intermediate scorpions climbed in legumes at a high frequency during January–April time-period, and the January–April time-period is when intermediate scorpions have the highest proportion of caterpillar prey of any time-period or size class (McReynolds 2020). This supports the implication that all size classes of scorpions climb into blackbrush or other legumes to forage for caterpillars and other prey found in the foliage and then feed in legumes but especially intermediate scorpions.

Important factors determining the diet of *C. vittatus* and the feeding rate by *C. vittatus* include foraging method, temporal shifts in prey availability, scorpion size and microhabitat use. Scorpions such as *C. vittatus* can forage using either ambush [sit-and-wait] or active search for prey, and the method used can determine what prey are caught (see McCormick & Polis 1990). Although active search by scorpions is considered rare and active search on vegetation has rarely been observed, buthids and other errant scorpions use vegetation more than other scorpion species and could be more active foragers on vegetation (see McCormick & Polis 1990). Hadley & Williams (1968) observed *Centruroides sculpturatus* Ewing, 1928 actively searching on rocks and vegetation. For *C. vittatus* to capture a high proportion of caterpillars, active search on vegetation, especially in blackbrush and other legumes, would be necessary.

I suggest that, at least for errant scorpions such as *C. vittatus*, the scorpion can switch between sit-and-wait and active foraging behavior when prey availability changes (see Formanowicz et al. 1991). However, prey availability does not always influence the activity of scorpions (Bradley 1988). Active foraging on vegetation by *C. vittatus* can explain why scorpions are capturing caterpillars that are sedentary and would rarely be encountered using sit-and-wait foraging. Active foraging by scorpions for caterpillars in legumes (e.g., blackbrush, guajillo or mesquite) can explain why a high proportion of scorpions with caterpillars were in blackbrush or other legumes and climbed higher than scorpions with orthopteran or intraguild prey (dangerous prey) or other prey in other vegetation.

Foraging on the ground versus vegetation.—Scorpions are usually considered ground foraging sit-and-wait predators (Shachak & Brand 1983; McCormick & Polis 1990) Many species of Buthidae (bark scorpions) such as *Mesobuthus gibbosus* (Brulle, 1832) (Kaltsas et al. 2008) and two species of buthids in leaf-litter, *Tityus pusillus* Pocock, 1893 and *Ananteris mauryi* Lourenco, 1982 (Lira et al. 2013, 2015), have been observed foraging only or mainly on the ground. *Centruroides vittatus* forage on vegetation but can still forage on the ground for certain prey that are more common there, including intraguild prey such as wolf spiders (Lycosidae) and Solifugae. Orthopterans can be common on the ground, but some, such as long-horn grasshoppers (Tettigonidae), are frequently on vegetation. Nevertheless, scorpions can forage for intraguild and orthopteran prey by the sit-and-wait method on the ground or on vegetation, because these prey are active on the ground or climbing on vegetation when foraging or changing microhabitats (Ramírez-Arce 2015; Nime et al. 2016; Visser & Geerts 2020). Foraging for moths and other nocturnal flying insects is by the sit-and-wait method and can be done on the ground or vegetation (Krapf 1988; McCormick & Polis 1990; Ashford et al. 2018). Activity on the ground by *C. vittatus* of all size classes is more frequent during May–August. Perhaps scorpions increase foraging on the ground because availability of prey such as caterpillars in legumes is lower during this time-period leading to lower activity in legumes during May–August for all size classes of scorpions. Future research will consider the effect of caterpillar availability in blackbrush on microhabitat use by the different size scorpions and over the seasons. In addition, scorpions could be more active on the ground because of increased quickness with higher temperatures could enhance pursuit of prey or escape from predators (Carlson & Rowe 2009). Therefore, scorpions can be foraging on the ground for dangerous (orthopterans and intraguild prey) and other prey through all months of the year but still foraging on vegetation when prey availability on vegetation is high.

Handling prey on vegetation vs. ground.—Scorpions with prey were rarely observed on the ground, and scorpions on vegetation were observed with a variety of prey including prey commonly found on the ground. Therefore, it is possible that prey are captured on the ground then carried into vegetation for consumption. Dangerous prey (intraguild and orthopteran

prey) could be easier to handle when carried into vegetation (Webber & Graham 2013; see Davison et al. 2020). However, *C. vittatus* appears to carry all prey captured on the ground into vegetation and consume prey captured on vegetation in the vegetation as well. It is assumed that scorpions carrying prey into vegetation from the ground or transferred from other vegetation will not climb as high as scorpions that forage and capture prey in the vegetation. The height of scorpions with prey on blackbrush or other legumes versus other vegetation supports the hypothesis that scorpions foraging for prey on legumes often remain high in the legumes to feed. On the other hand, scorpions that capture prey on the ground or in other vegetation do not carry that prey as high into vegetation.

Other possible functions of carrying prey to vegetation are to avoid intraguild predation (see Bradley & Brody 1984; Polis & McCormick 1986, 1987) or to avoid interference from ants and other kleptoparasites while feeding on prey (McReynolds 2008). Many burrowing scorpions carry prey to the burrow (Bub & Bowerman 1979; Kaltsas et al. 2008); prey is also carried into vegetation by juveniles but rarely by adults (Skutelsky 1996), perhaps because adults are not at risk of intraguild predation or interference. In contrast, all size classes of *C. vittatus* consume prey on vegetation and rarely on the ground, perhaps to avoid predation or interference.

Microhabitat quality.— For many species, microhabitat use and temporal differences in foraging activity and success can be determined by the risk of cannibalism (Hallander 1970; Polis 1988a; Wagner & Wise 1997; Rudolf 2007; Rudolf & Armstrong 2008). One hypothesis is that individuals with higher risk of predation (including cannibalism) will trade-off foraging success with use of a sub-optimal habitat or microhabitat (Mittelbach 1984; Werner & Hall 1988; Morse 2007) to reduce predation risk. It is predicted that the larger, more cannibalistic individuals will be in the high-quality microhabitat with higher foraging success (Murdoch & Sih 1978; Sih 1981, 1982; Wissinger et al. 2010). In *S. mesaensis*, intraguild predation can cause shift in habitat from the optimal sand dunes to the less optimal heterogeneous and hardpan habitat (Polis & McCormick 1987). For *C. vittatus* in south Texas, the data from this study suggest two possible hypotheses about quality microhabitats. The first hypothesis is that legumes (especially blackbrush) is the high-quality microhabitat, and the preferred prey are caterpillars; the second hypothesis is that succulents (prickly pear cactus, strawberry cactus, and other succulents) are the high-quality microhabitat and preferred prey are orthopteran and intraguild (dangerous) prey.

For the first hypothesis, there is evidence of higher foraging success (high feeding rate) in blackbrush and other legumes, but there is no evidence of a shift to another microhabitat by small or intermediate scorpions because of the risk of cannibalism (second prediction). In fact, intermediate scorpions have higher activity in blackbrush (and other legumes) than the large scorpions, especially in January–April, and intermediate scorpions have a higher proportion of caterpillars as prey during January–April (McReynolds 2020). This supports the first prediction of the hypothesis, but this pattern is counter to the second prediction that individuals with higher risk of predation, including cannibalism, will trade-off foraging success with a shift to sub-optimal microhabitats and time periods to reduce their risk of predation (Mittelbach 1984; Werner & Hall 1988). There is no evidence of this trade-off in the use of blackbrush and other legumes as the smaller scorpions apparently can avoid larger scorpions and still forage in blackbrush and other legumes. In fact, the large scorpions are not as active in legumes or other microhabitats during the January–April time-period even though it appears to be optimal time period for foraging for caterpillars (McReynolds 2020) Further study is needed to determine if this is because of the high abundance of blackbrush and other legumes, temporal shifts in the activity of scorpions, or smaller scorpions using the foliage and thinner branches more efficiently than larger scorpions. All size classes of scorpions use blackbrush and other legumes and have caterpillars as frequent prey.

For the second hypothesis, it is assumed that the high-quality microhabitat is succulents because large scorpions are present in succulents in a higher proportion than other size classes, especially during September–December. There is no support for the first prediction, high foraging success in succulents. Very few caterpillars or other prey were observed in succulents, and many scorpions observed feeding in succulents had orthopteran and intraguild prey that can be carried into the succulents from the ground. However, there is support for the second prediction. The large scorpions were in succulents at a higher frequency than small and intermediate scorpions, especially during September–December. The very high frequency of succulent use by large scorpions versus the smaller size classes cannot be explained by foraging success or prey availability, but succulents are possible refuges for *C. vittatus* (McReynolds 2008). A refuge is more important than prey availability for many arachnids (Marshall 1997; Bibbs et al. 2014; Corey & Hebets 2017), and for *C. vittatus*, prickly pear cactus and strawberry cactus may be high-quality microhabitat as a diurnal refuge (McReynolds 2008). Larger scorpions can deny smaller size classes access to the succulents because of the high risk of cannibalism for the smaller scorpions (McReynolds 2020). Further study is required to determine if larger scorpions deny smaller scorpions access to succulents.

Centruroides vittatus of all size classes use vegetation and the ground for various reasons. The uses of these microhabitats are not mutually exclusive, although microhabitats such as legumes can be more important in active foraging for caterpillars, and succulents as a refuge. All microhabitats can be used for sit-and-wait foraging and all vegetation for feeding. This can explain the high variance (high standard deviation) of heights in all vegetation types. The results showed that *C. vittatus* fed on prey in vegetation even if the prey was captured on the ground. The very high frequency of succulent use by large scorpions versus the smaller size classes cannot be explained by foraging success or prey availability. Legumes appear to be used more by intermediate scorpions for foraging for caterpillar prey, and succulents appear to be an important refuge for large scorpions; smaller scorpions appear to be denied access to succulents because of the risk of cannibalism by the large scorpions.

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