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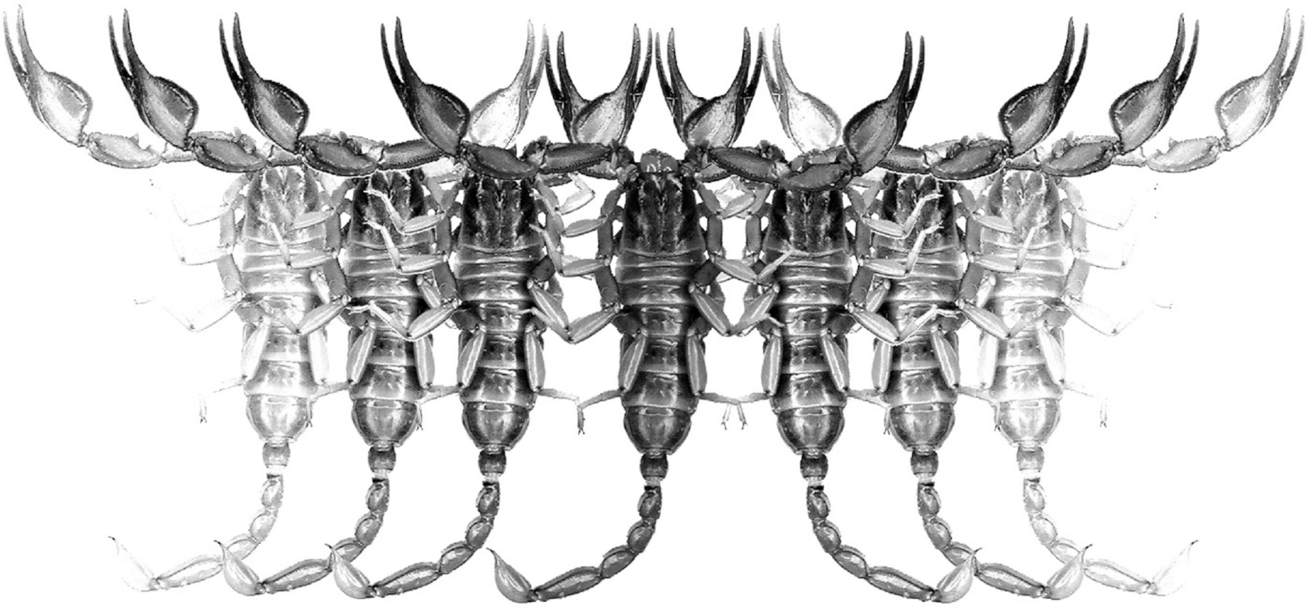

Effect of seasons and scorpion size on the foraging and diet of the striped bark scorpion, *Centruroides vittatus* (Buthidae: Scorpiones) in blackbrush habitat of south Texas

C. Neal McReynolds

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Derivatio Nominis

The name ***Euscorpius*** Thorell, 1876 refers to the most common genus of scorpions in the Mediterranean region and southern Europe (family Euscorpiidae).

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Effect of seasons and scorpion size on the foraging and diet of the striped bark scorpion, *Centruroides vittatus* (Buthidae: Scorpiones) in blackbrush habitat of south Texas

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Summary

Diet and foraging success of the striped bark scorpion, *Centruroides vittatus*, in South Texas are influenced by both scorpion size and season of the year. In the ten-year study of the striped bark scorpions in the blackbrush habitat of south Texas, the diet was variable with caterpillars (Lepidoptera) as the main prey for all seasons and all size classes of scorpions. The proportion of caterpillars did vary significantly with size class of scorpion and months of the year with intermediate size scorpions capturing more caterpillars during January–April than other size classes or months of the year. The proportion of orthopteran and intraguild prey was higher during September-December and for large scorpions. The height of scorpions was significantly different among prey types and scorpion size classes or prey types and months of the year. The median height of scorpions with caterpillar prey was significantly higher than scorpions with orthopteran or intraguild prey. The intermediate size scorpions with caterpillar prey and scorpions with caterpillar during January–April were higher in vegetation than scorpions with other prey, other size classes and/or months of the year. The foraging success of scorpions varied significantly with size class and month of the year. The highest foraging success was the intermediate size scorpions during January–April and the lowest was the large scorpions during January–April. However, the larger scorpions had the second highest foraging success during September–December. These results suggest that *C. vittatus* use both active search and ambush (sit-and-wait) foraging methods. The intermediate size scorpions capture more caterpillars than other size classes of scorpions by actively foraging in vegetation especially during January-April. The larger scorpions do not appear to interfere with the foraging success of intermediate or smaller scorpions even though cannibalism is observed.

Introduction

A number of factors influence foraging behavior and thus affects diet and foraging success of predators. The size and/or age of predator can determine foraging success by affecting type and effectiveness of foraging method and diet (Cisneros & Rosenheim, 1997; Smith & Petranka, 1987;). Temporal changes including changes in prey availability and the activity of the predator can also influence foraging success. Prey availability can shift with seasonal changes (Vonshak et al., 2009). Spider activity can change over time with seasonal increases in prey availability, but spatial and temporal differences in prey availability at the local level or short time scale are not predictable and the spiders cannot track the fluctuations (Bradley, 1993).

The size and age of the forager can affect the forager's risk of predation or interference from other foragers such as interference competition (Geraldi, 2015). Foraging by a predator can be influenced by cannibalism and intraguild predation because of the risk of predation for smaller sizes and change in diet and foraging success for larger size predators with a switch to cannibalism and intraguild predation (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).

Cannibalism can lead to habitat or temporal shifts by the more vulnerable (smaller) predators (Murdoch & Sih, 1978; Sih, 1981, 1982; Polis, 1980a, 1984). In addition, predation by large predators can shift because of the growth of the successful cannibal or intraguild predator leading to predation on other larger prey by increasing size of the predator (Polis, 1988a; Persson et al., 2000; Rudolf, 2006, 2007; Rudolf & Armstrong, 2008; Takatsu & Kishida, 2015). Larger or older individuals can exclude smaller or younger individuals from optimal time or habitat including 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, 1987). Ontogenetic dietary shifts between smaller size classes and the large adults because of cannibalism could prevent intraspecific competition between size classes (Wissinger et al., 2010). Risk of predation can mean that smaller more vulnerable individuals shift to lower quality habitats (lower quality prey or low prey availability) to avoid predators and thus reduce foraging success or change diet (Mittelbach, 1984; Werner & Hall, 1988). The early instars of arthropods will avoid optimal habitats and reduce foraging activity in the presence of larger juveniles and adults to avoid cannibalism (Murdoch & Sih, 1978; Sih, 1981, 1982; Zimmermann & Spence, 1998).

Low metabolic rate of scorpions can contribute to foraging behavior of scorpions especially cannibalism and intraguild predation with juvenile scorpions being an important prey item for adults and larger juvenile scorpions (Lighton et al., 2001). Examples of scorpion size (and age) influencing activity in the sand scorpion, *Smeringurus mesaensis* (Stahnke, 1957) (formerly *Paruroctonus mesaensis*) includes age affecting 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 at different ages: temperature (Polis, 1980a) and prey abundance (Polis, 1980a, 1988b). Intermediate age *S. mesaensis* have high activity at lower temperatures and lowest activity at higher temperatures where adults and the youngest scorpions are more active (Polis, 1980a). The surface density of adult *S. mesaensis* is directly correlated with prey abundance, but the intermediate and younger age classes are negatively correlated with prey abundance (Polis, 1980a, 1988b). Adult *S. mesaensis* utilize the optimal habitat (sand dunes) and juvenile *S. mesaensis* and heterospecific scorpions utilize the sub-optimal habitat (hard pan) because of intraguild predation (Polis & McCormick, 1987). However, a temporal shift between juveniles and adult females does not occur for *Paruroctonus utahensis* (Williams, 1968), but juveniles were more likely to climb in vegetation than adults even though it was rare for all age classes (Bradley, 1988). Juvenile *Buthus occitanus* (Amoreux, 1789) forage in vegetation at higher frequency than adult *B. occitanus* and adult activity shifts with lunar cycle and juvenile activity does not (Skutelsky, 1996).

In earlier studies of the study animal, *Centruroides vittatus* (Say, 1821) (Scorpiones; Buthidae), it was observed that more juveniles than adults climb in vegetation and climb higher (Brown & O'Connell, 2000), and temporal differences in surface activity of *C. vittatus* and ontogenetic shifts occur in the activity of scorpions (McReynolds, 2012). Caterpillars are important prey items for *C. vittatus* in South Texas, and scorpions are often observed feeding on caterpillars (McReynolds, 2008). Comparisons among different size classes of scorpions and time periods will be performed to determine type of prey in the diet, activity and the foraging success. The height of scorpions with different types of prey will be compared. These comparisons will be to determine possible preferences in diet and changes in foraging behavior among scorpion size classes and seasonal time periods.

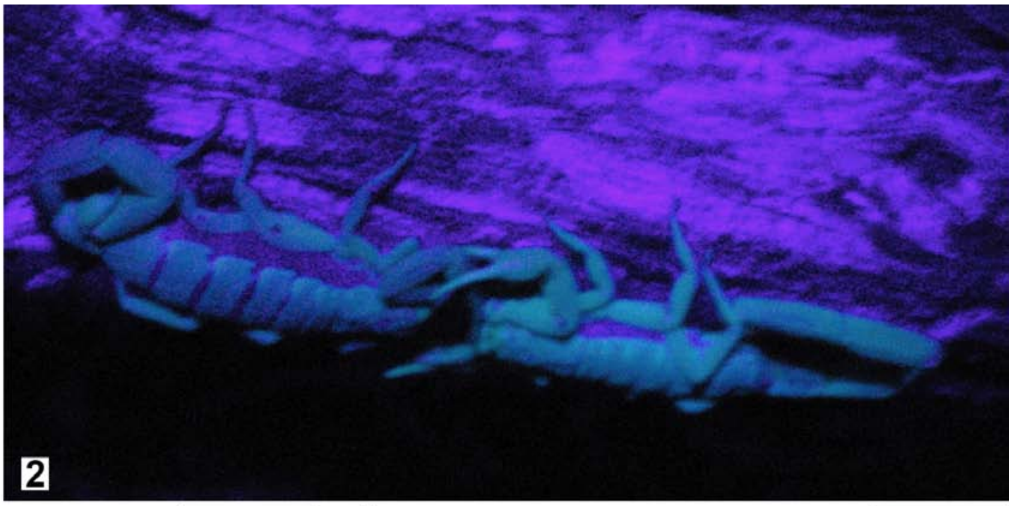
Methods

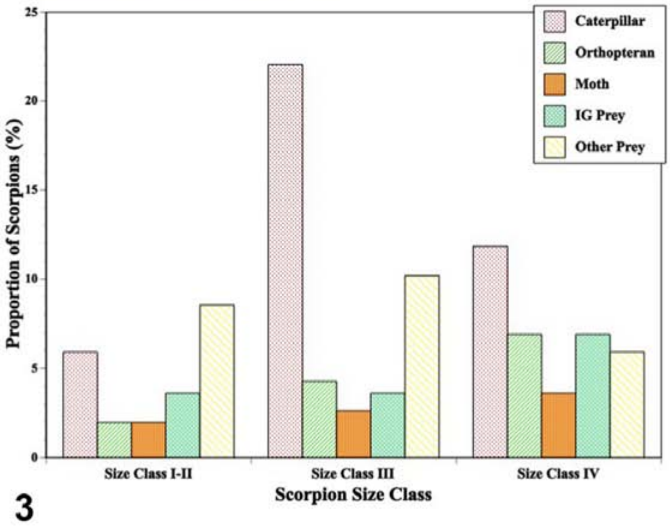
Centruroides vittatus (Say, 1821) has a wide distribution with Laredo, Texas in the southern portion of the species' range (Shelley & Sissom, 1995). *C. vittatus* is nocturnal with refuges during the day in debris, beneath vegetation, under bark, and in holes in the ground, but *C. vittatus* and other bark scorpions rarely dig their own burrows (Polis, 1990) and none were observed digging a burrow in this study (pers. obs.). 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 the age of maturity between 36 and 48 months (Polis & Sissom, 1990). On nights of emergence, *C. vittatus* active on the ground and/or in vegetation will be observed. Both courtship by *C. vittatus* and females carrying first instars have occasionally been observed in the field (pers. obs.). Voucher specimens of *C. vittatus* were deposited in the invertebrate collection at Texas A&M International University.

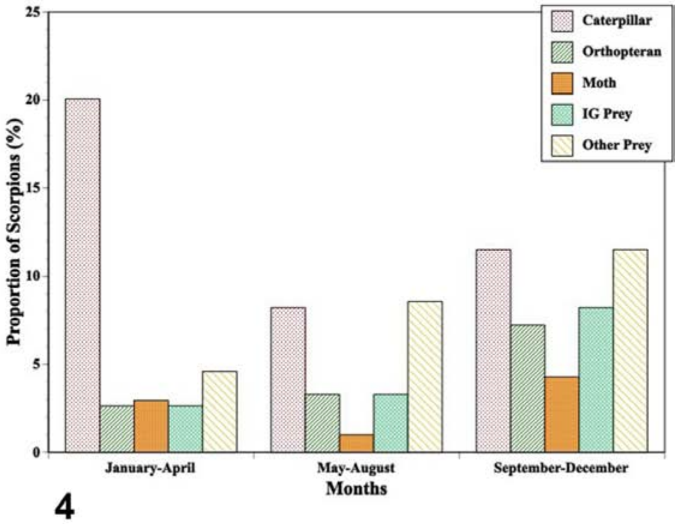
The size of *C. vittatus* was estimated using size classes. This is similar to the method used to estimate age classes for *S. mesaensis* (Polis, 1980a, 1984; Polis et al., 1985). Size classes of *C. vittatus* were based on estimates of the length of the scorpion from the anterior of the prosoma to the posterior of the mesosoma (Fig. 1). This measurement of scorpion size was used for *S. mesaensis* (Polis & McCormick, 1987). 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 (McElroy et al., 2017). Size class IV scorpions included adult males and females but some penultimate instars were included in size class IV. Size class I scorpions included second instar scorpions after molting from first instar scorpions that are on the dorsal mesosoma of the female scorpion after birth (Polis & Sissom, 1990). Other size classes do not correspond to instars or age classes. An association between size and age is not possible at this time for *C. vittatus* in south Texas because the life history of *C. vittatus* has not been determined for south Texas and the birth period is not discrete (Polis, 1984). The estimates of age to maturity is 36 to 48 months (Polis & Sissom, 1990), but this cannot be associated with size estimates.

This study was done on the campus of Texas A&M International University (27°35'N 99°26'W), Laredo, Texas. Laredo is located in the Tamaulipan Biotic Province that is 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 (*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*), etc.

Scorpions were observed at night by locating the individual scorpions fluorescing under ultraviolet light (Fig.





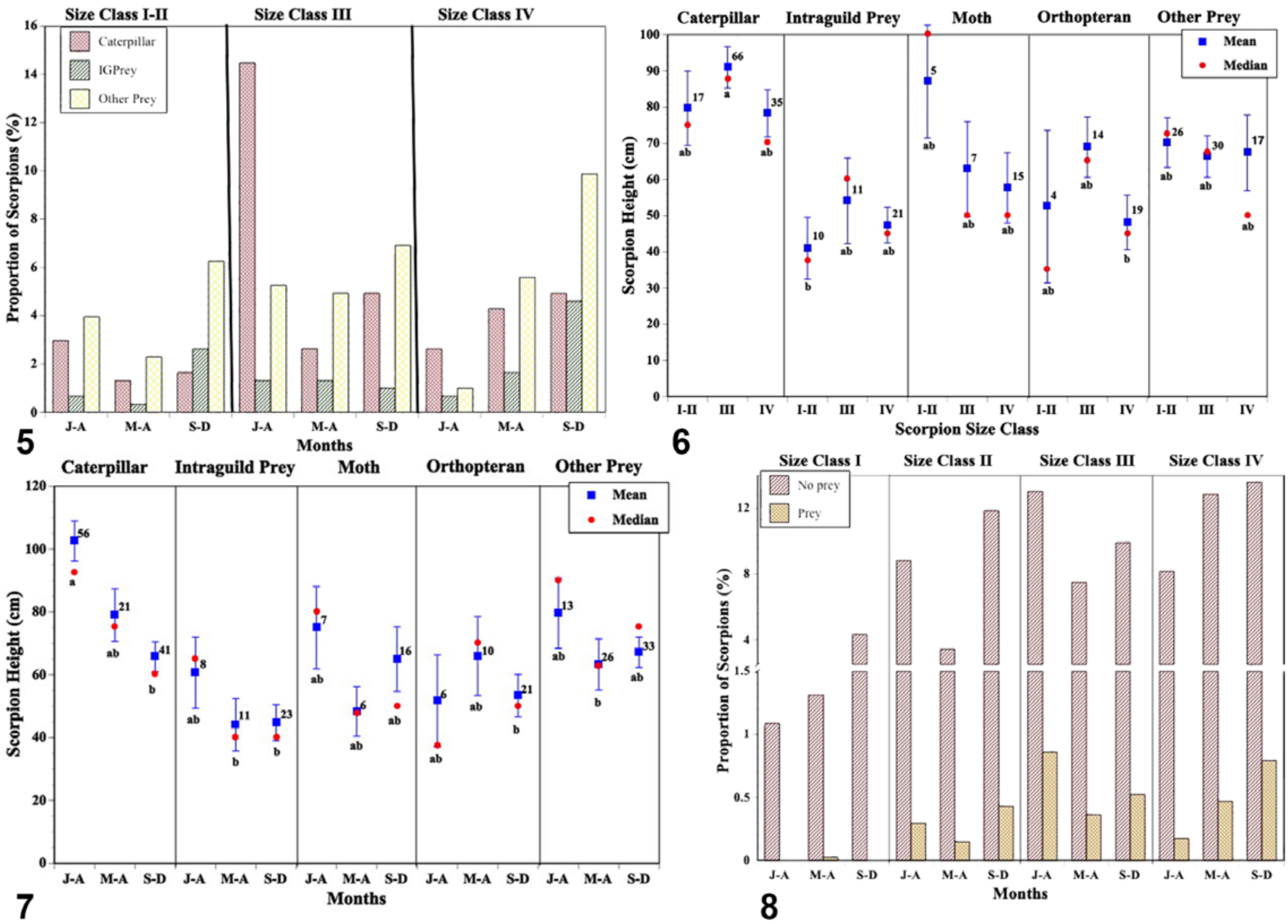


Figures 1–4:. **Figure 1**. *Centruroides vittatus* length estimated from length of the scorpion from the anterior of the prosoma (P) to the posterior of the mesosoma (M). **Figure 2**. Male and female *C. vittatus* courting on branch of a tree fluorescing under ultraviolet light. **Figure 3**. The proportion (%) of *C. vittatus* with different prey types among scorpion size classes. Size classes I and II were pooled for the statistical analysis. The frequency of scorpions for different prey types was significantly different among size classes ($G = 28.091$, $P < 0.001$, $df = 8$, $n = 304$). IG Prey = Intraguild prey. See Table 1 for planned comparisons among prey types. **Figure 4**. The proportion (%) of *C. vittatus* with different prey types among months of the year. The frequency of scorpions for different prey types was significantly different among months ($G = 36.596$, $P < 0.001$, $df = 8$, $n = 304$). Months of the year pooled. IG Prey = Intraguild prey. See Table 2 for planned comparisons among prey types.

2) (Sissom et al., 1990). Observed scorpions were out of their refuges and active in various microhabitats. No data were collected on scorpions in their refuges to avoid destruction of the habitat. Data on scorpion 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 site. 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 if in vegetation, if the scorpion had prey or not and prey taxa. All months of a year 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.

Prey capture by scorpions can be observed as scorpions digest externally, thus prey items can be observed in pedipalps or chelicerae (Polis, 1979). The prey captured were placed in the following classes: no prey captured, caterpillars (Lepidoptera larvae), Orthoptera, moths (adult Lepidoptera), IGP (intraguild prey including Scorpiones, Araneae, Solifugae, Opiliones, Mantodea and Chilopoda) and other prey. Foraging success can be measured as the number of scorpions with prey per total number of scorpions (scorpions with no prey and with prey) observed for each night or class. Foraging success is the same as feeding rate as described for *S. mesaensis* (Polis, 1979; McCormick and Polis, 1990).

Contingency tables were analyzed using the two-way and three-way G-tests of independence to compare prey capture, scorpion size classes and months of the year (Sokal & Rohlf, 1981). The data were pooled on several occasions



Figures 5–8: **Figure 5**. The proportion (%) of *C. vittatus* with different prey types among months of the year and scorpion size classes (n = 304). Months of the year pooled with J-A = January through April, M-A = May through August and S-D = September through December. IG Prey = Intraguild prey. See Table 3 for a three-way G test of the contingency table among prey types, months of the year and scorpion size classes. **Figure 6**. The mean and median height of *C. vittatus* on vegetation with different prey types among scorpion size classes. Standard error bar (± 1 SE) and sample size (n) were shown for the mean of each class. Median scorpion height was significantly different among prey types (Kruskal-Wallis Statistic: KW = 44.671 (corrected for ties), $P < 0.001$). Medians with the same letter were not significantly different in unplanned comparisons using Dunn's Multiple Comparisons Test. **Figure 7**. The mean and median height of *C. vittatus* on vegetation with different prey types among months of the year. Standard error bar (± 1 SE) and sample size (n) were shown for the mean of each class. Months of the year pooled with J-A = January through April, M-A = May through August and S-D = September through December. Median scorpion height was significantly different among prey types (Kruskal-Wallis Statistic: KW = 56.157 (corrected for ties), $P < 0.001$). Medians with the same letter were not significantly different in unplanned comparisons using Dunn's Multiple Comparisons Test. **Figure 8**. The proportion (%) of *C. vittatus* with no prey versus scorpions with prey among months of the year and scorpion size classes (n = 7451). Size classes I and II were shown in the figure but pooled for the statistical analysis. Months of the year pooled with J-A = January through April, M-A = May through August and S-D = September through December. See Table 4 for a three-way G test of the contingency table among no prey or prey, months of the year and scorpion size classes.

because the G-test cannot be performed when a value in the table is zero. It was necessary to pool size class I scorpions with size class II scorpions when comparing prey because size class I scorpions were rarely observed with prey. The months of the year were pooled because January, February and December had zero scorpions observed with prey. For the three-way G-tests, the prey classes orthopterans and moths had to be pooled with other prey when comparing prey capture versus scorpion size classes versus months of the year and all preytypes were pooled as prey when comparing no prey versus prey. The height of scorpions on vegetation with different prey types were compared using the Kruskal-Wallis test. The non-parametric Kruskal-Wallis test was performed instead of the Analysis of Variance (ANOVA) test because some assumptions of ANOVA test such as equal standard deviations between classes and normality for all classes were not meet (Sokal & Rohlf, 1981). A unplanned comparison using Dunn's multiple comparisons was performed when the Kruskal-Wallis test was significant.

Results

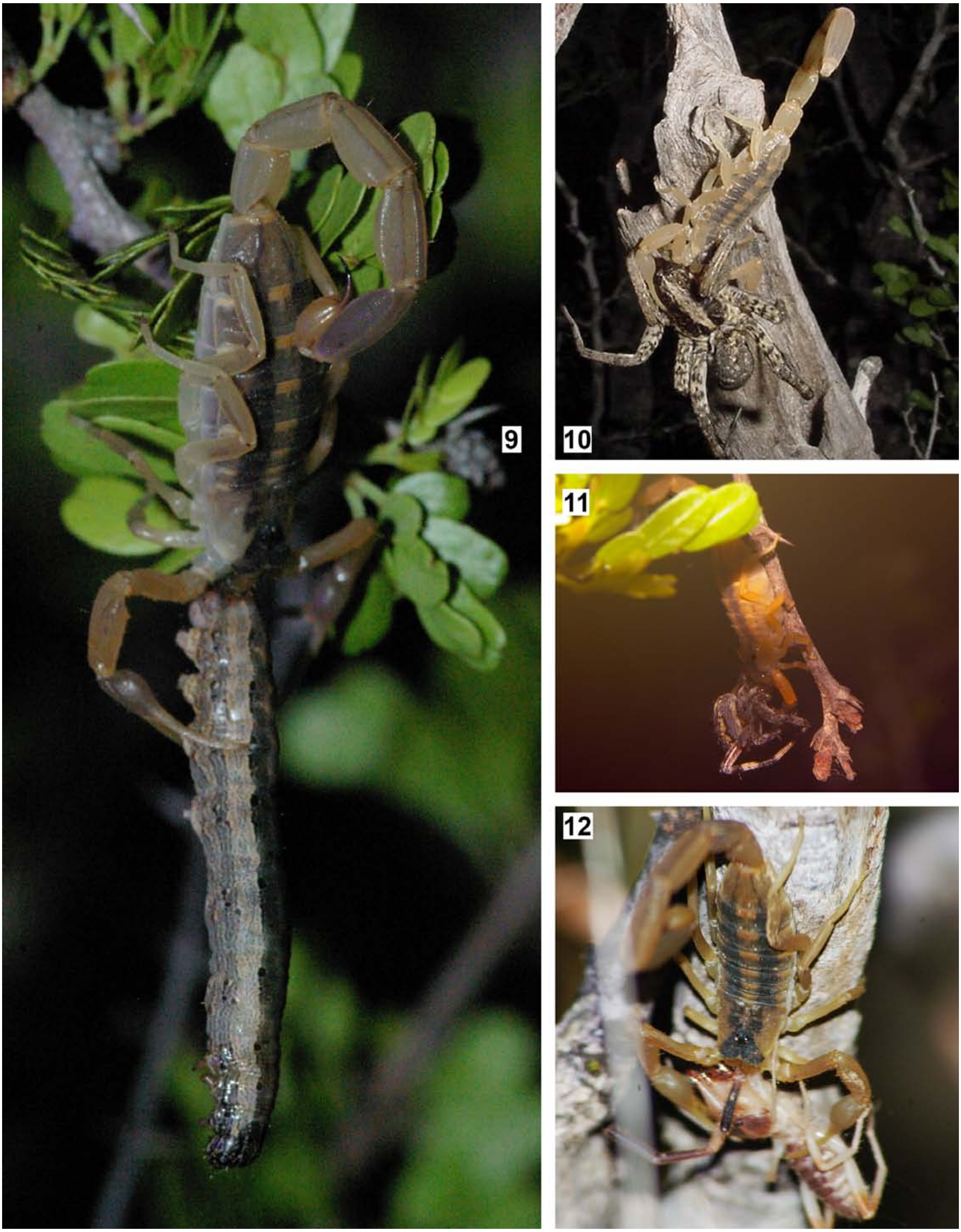
The taxa of prey captured by *C. vittatus* changed with size of the scorpion and the season of the year. There was a significant difference in type of prey with size class of scorpion (Fig. 3). In the planned comparison of caterpillar versus all other prey, there was a significant difference with higher proportion of caterpillar prey for size class III than other size classes (Fig. 3, Table 1). The planned comparison of orthopteran and intraguild prey versus and moth and other prey was significantly different (Table 1). There was higher proportion of orthopteran and intraguild prey for size class IV than other size classes (Fig. 3). Intraguild prey included cannibalism with two cases of cannibalism of the 65 prey captured (3.08%) by size class II scorpions and with six cases of cannibalism of the 107 prey captured (5.61%) by size class IV scorpions. Size class I and III scorpions had zero cases of cannibalism from the two or 130 prey captured respectively. The planned comparisons of orthopteran versus intraguild prey and moth versus other prey were not significantly different (Table 1). The proportion of size class I scorpions with prey (foraging success) was the lowest with 0.398% (n = 502), of size class II scorpions was 3.49% (n = 1863), of size class III scorpions was the highest with 5.42% (n = 2398) and of size class IV scorpions was 3.98% (n = 2687). There was a significant difference among size classes of scorpions with size classes I and II pooled in a contingency table for scorpions with prey versus no prey ($G = 20.6$, $P < 0.001$, degrees of freedom = 2). In the comparison of size class I versus size class II scorpions, there was a significant difference in scorpions with prey versus no prey ($G = 19.62$, $P < 0.001$, degree of freedom = 1).

The type of prey captured by the scorpions had a significant association with time periods of the year (three four month time periods) (Fig. 4). There was a very significant difference between caterpillars versus all other prey in planned comparison (Table 2). There was higher proportion of caterpillars in January–April than the other time periods (Fig. 4). The planned comparisons of orthopteran and intraguild prey versus moth and other prey and orthopteran versus intraguild prey were not significantly different (Table 2). Moth versus other prey was significantly was significantly different (Table 2). There was a low proportion of moths during May–August (Fig. 4). The proportion of scorpions with prey during January–April was 4.09% (n = 2418), of scorpions during May–August was 3.85% (n = 1944), and during September-December was 4.21% (n = 3087). There was not a significant difference among time periods in the contingency table for scorpions with prey versus no prey ($G = 0.39$, not significant, degrees of freedom = 2).

In a comparison of prey captured in relation to scorpion size class and months of the year, the highest proportion of caterpillars was captured by size class III scorpions during January-April and the highest proportion of intraguild prey were capture by size class IV scorpions during September-December (Fig. 5). The interaction comparison of the three-way G test was not significantly different (Fig. 5, Table 3). The conditional comparison of prey types versus months of the year with scorpion size classes at given levels was significantly different (Fig. 5, Table 3). A high proportion of caterpillars were captured by scorpions during January–April, and a high proportion of intraguild prey were captured during September–December (Fig. 5). The conditional comparison of scorpion size classes versus months of the year with prey types at given levels was significantly different (Table 3). Size class III scorpions had highest proportion of caterpillar, intraguild prey and other prey during January–April, and size class IV scorpions had highest proportion of intraguild prey and other prey and a high proportion of caterpillar prey during September–December (Fig. 5). The conditional comparison of prey types versus scorpion size classes with months of the year at given levels was not significantly different (Table 3). At the given months of the year, a high proportion of caterpillars were prey for both size classes III and IV scorpions during January–April, and a high proportion of intraguild prey were captured by size classes I-II and IV scorpions during September–December (Fig. 5).

The mean, median and standard error for heights of scorpions on vegetation among different types of prey varied among scorpion size classes (Fig. 6) or months of the year (Fig. 7). Medians among different types of prey and scorpion size classes were significantly different using the non-parametric Kruskal-Wallis test (Fig. 6). The median height of size class III scorpions with a caterpillar was significantly higher than size class I-II scorpions with orthopteran or size class IV scorpions with intraguild prey using Dunn's multiple comparisons test (Fig. 6). In comparison among the months of the year, the medians were significantly different among different types of prey (Fig. 7). The height of scorpions with caterpillar prey during January–April was significantly higher than scorpions during September–December with either caterpillar prey, orthopteran prey and other prey and scorpions with intraguild prey during both January–April and May-August (Fig. 7). If scorpions of different size classes (and months of the year) were pooled for the different prey types, the median heights of scorpions were significantly different (Kruskal-Wallis Statistic KW = 35.114 (corrected for ties), $P < 0.001$). Scorpions with caterpillar prey were significantly higher than scorpions with orthopteran and intraguild prey and scorpions with other prey significantly higher than intraguild prey (Dunn's multiple comparisons test).

A comparison of scorpions among prey versus no prey (foraging success), scorpion size classes and months of the year showed significant associations (Fig. 8). The interaction comparison for the three-way G-test was significant (Table 4). Size class III scorpions had the highest proportion of prey or high foraging success and the lowest proportion of prey was size class IV scorpions both during January–April (Fig. 8). In addition, size class IV scorpions during September-December had the second highest proportion of prey (Fig. 8). Conditional comparison of size classes of scorpions versus months of the year with prey or no prey at given levels was



Figures 9–12. *Centruroides vittatus* with caterpillar (Lepidoptera) prey on blackbrush (*V. rigidula*) (9), with intraguild prey, wolf spider (Lycosidae: Araneae) (10), with an intraguild prey, orb-web spider (Araneidae: Araneae) (11), and with an intraguild prey, Solifugae (12).

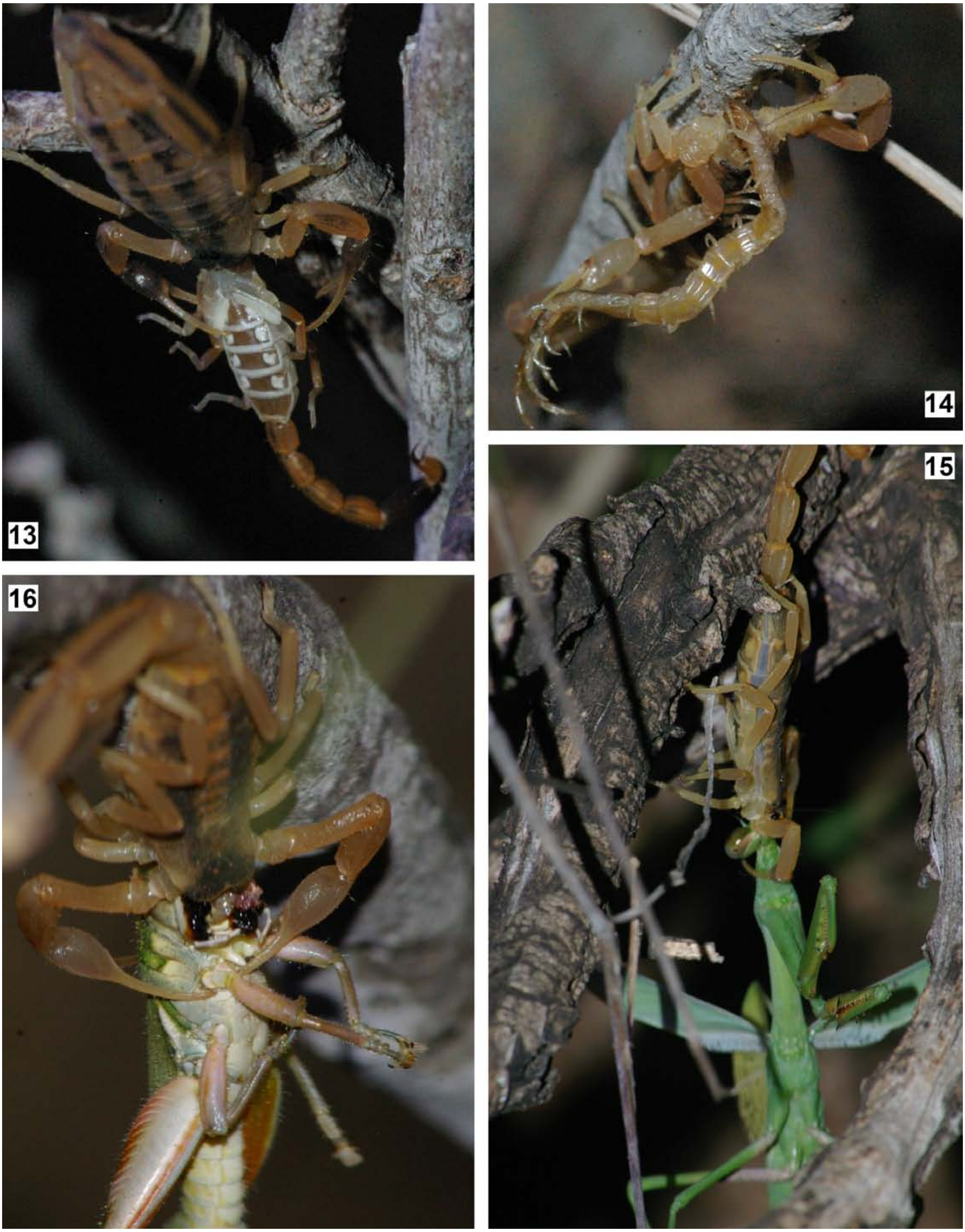
very significantly different (Table 4). The activity of scorpion size classes differed with time period for both scorpion with prey and no prey (Fig. 8). Size class I scorpions had the highest activity during September-December with activity low for the other two time periods. Both size class II and III scorpions had reduced activity during May-August, but size class II scorpions had higher activity during September–December and size class III scorpions higher during January–April. Size class IV scorpions had lower activity in January-April and high activity during the other two time periods (Fig. 8). Conditional comparison of time period versus prey or no prey with scorpion size classes at given levels was significantly different (Table 4). The proportion of scorpions with prey was lower for May–August for size class III and IV scorpions but not size class I and II scorpions (Fig. 8). Conditional comparison of scorpion size class versus prey or no prey with time periods at give levels was significantly different (Table 4). Size class III scorpions had a higher proportion of prey (foraging success) than size class I and II scorpions even when pooled (Fig. 8). The proportion of prey for size class IV scorpions varied with time period with low foraging success during January–April and high during September–December (Fig. 8).

Discussion

The type of prey in the diet is similar for all size classes of scorpions (with size class I-II pooled) and different time periods (four-month periods) during the year, but there are differences in proportion of prey for size classes of scorpions and time periods. Caterpillars are important prey item for *C. vittatus* at all time periods and all size classes but higher in January-April and for size class III (McReynolds, 2008). The diet of scorpions is broad with many arthropod species but caterpillars are a rare prey item in most scorpion studies (McCormick & Polis, 1990; Polis & McCormick, 1986). The diet of *S. mesaensis* includes a variety of prey with the most frequent prey being beetles with caterpillars rare (n = 792), and most of the biomass consumed is from conspecifics and other scorpion species (Polis, 1979). There is a significant difference in diet and size of prey for different age classes of *S. mesaensis* as well (Polis, 1979). Diet of *Aegaeobuthus gibbosus* (Brullé, 1832) (formerly *Mesobuthus gibbosus*) a burrowing buthid with sit-and-wait foraging behavior on the ground had either Diptera at Crete (n = 24) or Lepidoptera adults at Koufonisi (n = 29) as the most frequent prey items and larva (taxa not identified) were rare (Kaltsas et al., 2008,). In Arkansas, *C. vittatus* rarely feed on caterpillars with intraguild prey including spiders and cannibalism being the main prey items (n = 43) (Yamashita, 2004). In this study, caterpillars (Lepidoptera) (Fig. 9) were the main prey item for size class III and IV scorpions with the intermediate size of scorpions capturing more caterpillars than the larger scorpions. Other prey for the larger scorpions included intraguild prey [e.g., Araneae (Figs. 10, 11), Solifugae (Fig. 12), cannibalism on other scorpions (Fig. 13), Chilopoda (Fig. 14) and Mantodea (Fig. 15)], Orthoptera (Figs. 16, 17), adult moths (Lepidoptera) (Fig. 18) and other prey (Fig. 19). The higher proportion of intraguild prey by the larger scorpions of south Texas is a similar pattern to the older age class of *S. mesaensis* having a higher proportion of cannibalism (Polis, 1979). In Polis (1979), the highest proportion of scorpions with prey is the youngest age class. The intermediate size (size class III) scorpions have the highest proportion of prey in this study. Observations of size class I scorpions with prey are rare with only two size class I scorpions with prey observed. The possible explanations include difficulty in observing small prey. Alternatively, the size class I scorpions seek more sheltered areas to feed after capturing prey perhaps to avoid disturbances by other predators and individuals stealing food such as ants (McReynolds, 2008). These factors can explain why size class I scorpions were not observed with caterpillar prey and very rarely with other prey.

Important factors determining the diet of *C. vittatus* and the foraging success by *C. vittatus* include foraging method, temporal shifts in prey availability, scorpion size and microhabitat use. Scorpions can use either search method (ambush [sit-and-wait] or active search) for foraging and the method used can determine what prey are caught (McCormick & Polis, 1990). Most scorpion species forage on the ground and more often use sit-and-wait method in or near a burrow (Shachak & Brand, 1983; McCormick & Polis, 1990). Many species of scorpions have been observed foraging only or mainly on the ground such as *Aegaeobuthus gibbosus* (see Kaltsas et al., 2008) or two other species of buthids, *Tityus pusillus* Pocock, 1893 and *Ananteris mauryi* Lourenco, 1982 in leaf-litter (Lira et al., 2013). Active search by scorpions is considered rare and active search in vegetation has rarely been observed, but buthids and other errant scorpions use vegetation more and could be more active foragers in vegetation (McCormick & Polis, 1990). Hadley & Williams (1968) did observe *Centruroides sculpturatus* Ewing, 1928 actively searching on rocks and vegetation. For *C. vittatus* to capture a high proportion of caterpillars, active search in vegetation would be necessary because caterpillars are sedentary and usually remain in the vegetation. Shachak & Brand (1983) predict that burrowing sit-and-wait scorpions will disperse or remain inactive when prey availability is low instead of switching to active search. However, *Diplocentrus peloncillensis* Francke, 1975 (Diplocentridae) did switch from active search to sit and wait with an increase in prey availability (Formanowicz et al., 1991), but prey availability does not always influence the activity of scorpions (e.g., *P. utahensis* (Bradley, 1988)).

For *C. vittatus*, scorpions can forage in vegetation for caterpillars and other prey that are common in vegetation and on the ground for certain prey that are more common on the ground including intraguild prey such as wolf spiders (Lycosidae) and Solifugae. Orthopterans can be common on the ground but some such as longhorn grasshoppers (Tettigoniidae) are frequently in vegetation. Nevertheless, scorpions can forage for these orthopteran and intraguild prey on the ground by sit-and-wait method because these preys are



Figures 13–16. *Centruroides vittatus* with an intraguild prey, cannibalism by size class IV scorpion feeding on size class III (13), with an intraguild prey, centipede (Chilopoda) (14), with an intraguild prey, mantid (Mantodea) (15), and with grasshopper (Orthoptera) prey (16).

active on the ground when foraging or changing microhabitats. Foraging for moths and other nocturnal flying insects is by sit-and-wait method and can be done on the ground or vegetation (Krapf, 1988; McCormick & Polis, 1990; Ashford et al., 2018). In addition, *C. vittatus* could be more active during May–August because of increased quickness with higher temperatures to pursue prey or escape predators (Carlson & Rowe, 2009). However, the frequency of orthopterans and intraguild prey is higher in September–December time period than any other time period. Size class IV scorpions can be foraging on the ground for orthopterans and intraguild prey (including cannibalism) during September–December but still foraging in vegetation for caterpillars as well. Another possible explanation for the varied diet in *C. vittatus* besides prey availability is scorpions balancing nutritional demands as in balance between proteins and lipids (Raubenheimer et al., 2007) or essential nutrients and toxins (Toft, 1999). This could explain high caterpillar numbers in size class III scorpions because of different nutrient demands for high activity early in the year (Raubenheimer et al., 2007).

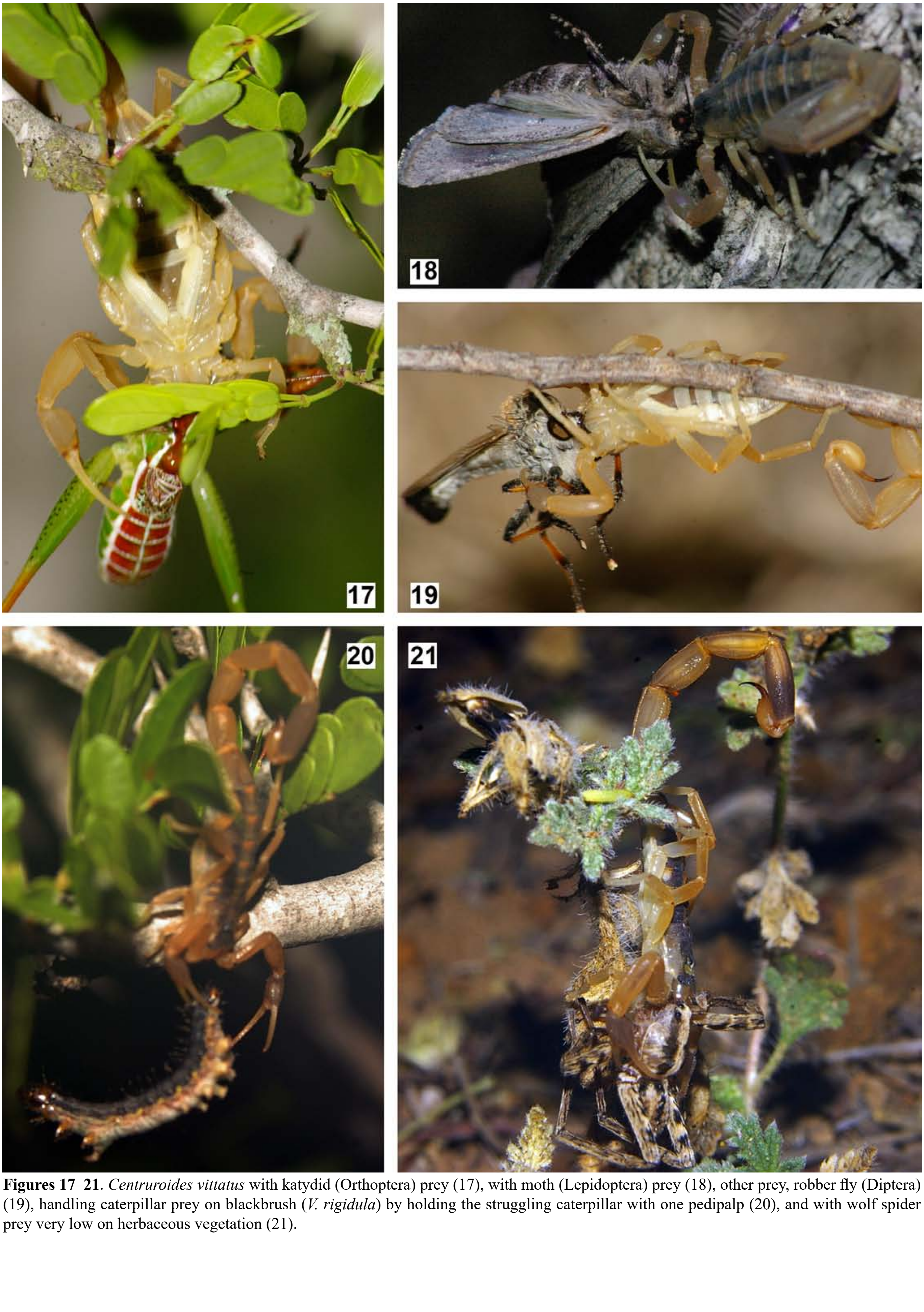
Brown & O'Connell (2000) hypothesize that *C. vittatus* climb in vegetation to either to reduce risk of predation or to forage in vegetation. Additional hypotheses for *C. vittatus* climbing in vegetation include errant scorpions such as *C. vittatus* using vegetation as a diurnal refuge (McReynolds, 2008, 2012) and *C. vittatus* feeding in vegetation (Brown & O'Connell, 2000). Most of the scorpions observed with prey were in vegetation, but the height in vegetation did vary with the prey type. Therefore, this supports use of vegetation by scorpions for feeding, but does not exclude either the foraging in vegetation or reducing risk of predation hypotheses.

Instead, the main reason for feeding in vegetation can depend on the type of prey captured. Some prey types (e.g., caterpillars) are more abundant and available in vegetation, and scorpions can capture the prey in vegetation and remain to feed. The scorpions with caterpillars are significantly higher than scorpions with intraguild prey or orthopterans. Size class III scorpions with caterpillar prey and scorpions with caterpillar prey during January-April were higher in vegetation than other classes. These results are related because a high proportion of scorpions with caterpillar prey were size class III scorpions during January-April. This suggests that scorpions climb into vegetation to actively forage for caterpillars in the foliage (Fig. 20) and often remain in the vegetation to feed, and this occurs mainly during January-April by size class III scorpions.

Other prey types (e.g., most intraguild prey) are abundant and available on the ground, and scorpions can capture the prey on the ground and then carry them into vegetation to feed. Webber & Graham (2013) suggests for *C. sculpturatus* when feeding on a centipede in vegetation the scorpion will feed with the prosoma down is to subdue a dangerous prey. Dangerous prey can include orthopteran and intraguild prey. However, I suggest that since the behavior of feeding with prosoma down is more common than just dangerous prey (pers. obs. and Figs. 2, 9-21), then the function of feeding with prosoma down in vegetation can be to reduce interference from struggling prey including less dangerous prey such as caterpillars. This still can be the main reason that scorpions carry prey such as orthopteran and intraguild prey (both can be dangerous prey) into vegetation, but the scorpion will not have to carry the prey from the ground very high in the vegetation to subdue the prey for feeding (Fig. 21). This can explain why scorpions with orthopteran and intraguild prey were lower than scorpions with caterpillars. The assumption is that scorpions will not climb as high when carrying a prey item. However, the mean height of scorpions for all prey types in both comparisons (Figs. 6 and 7) is greater than 40 cm, and the variance of scorpion heights for all prey types is high (not the high standard error for all prey types). One explanation for *C. vittatus* climbing higher (or remaining high) in vegetation to feed is to avoid predators and other interference while feeding (Brown and O'Connell, 2000; McReynolds, 2008). If this is to avoid larger conspecifics that are less agile climbers, then smaller scorpions could be higher in vegetation while feeding. This is not supported by the height of scorpions because heights were not significantly different among size classes for each of different prey types using unplanned comparisons. Although scorpions with caterpillar prey during September-December were significantly lower than scorpions with caterpillar prey during January-April with the unplanned comparison. This could be due lower risk of predation during September-December, but other explanations are possible including caterpillars are captured lower in vegetation by the larger scorpions in September-December. None of the explanations or any other possibility has been tested at this time.

Dangerous prey could still be a threat or can escape before the scorpion can begin feeding prosoma down so envenomating can be key to reduce the risk of escape or damage to the scorpion. Note the scorpion with the centipede in Fig. 14 has the prosoma perhaps to carry the centipede into vegetation to feed. The tactics of prey capture by the scorpion could depend on the risk of escape or damage from the prey (Bartos, 2007; Hadley & Williams, 1968). This could determine when the scorpion stings (Rein, 1993) and uses venom (Edmunds & Sibly, 2010). The efficiency of smaller scorpions in capturing prey could be lower than large scorpions perhaps because of the sting (Webber & Rodriguez-Robles, 2013) or difference in venom potency (McElroy et al., 2017). Intraguild prey (more dangerous) and orthopterans (more difficult prey) could require specific venoms for capture (McElroy et al., 2017). Although, variability in venom could be because of predator defense and not prey capture (Miller et al., 2016). Size class IV scorpions do capture more orthopterans and intraguild prey than the other size classes. One explanation for this dietary shift is that larger scorpions can handle these more dangerous or difficult prey perhaps because of larger size of pedipalps and stinger or more effective venom (higher dose, more potent or venom specific for these prey) (McElroy et al., 2017).

The seasonal activity of *C. vittatus* in West Texas roughly fits the pattern observed in this study with juveniles more



Figures 17–21. *Centruroides vittatus* with katydid (Orthoptera) prey (17), with moth (Lepidoptera) prey (18), other prey, robber fly (Diptera) (19), handling caterpillar prey on blackbrush (*V. rigidula*) by holding the struggling caterpillar with one pedipalp (20), and with wolf spider prey very low on herbaceous vegetation (21).

active than adults (male and female) in early months of the year and all scorpions less active in midsummer months (Brown et al., 2002). However, another buthid had a peak activity for adults and juveniles in August and September in Cuba (Cala-Riquelme & Colombo, 2011). Similarly, size class IV scorpions have a peak in activity with more prey captured in September–December but nearly as high of activity in May–August. The temporal differences in prey type are due to ontogenetic shifts in part for a spider (Howell & Ellender, 1984) and a scorpion (Polis, 1979), There are ontogenetic and seasonal differences in diet for *C. vittatus.* However, caterpillars are a main prey item for the three larger size classes of scorpions during all time periods. Seasonal changes affect prey availability and this affects the foraging behavior of spiders (Muotka, 1993; Crouch & Lubin, 2000) and scorpions (Araujo et al., 2010). Seasonal prey capture rates for *S. mesaensis* peak during periods of high prey availability (Polis, 1979, 1988b). Capture of caterpillars especially by size class III scorpions during January-April can peak because of high caterpillar availability during March and April because of the new foliage increasing the activity of caterpillars. Most of the caterpillars captured during this period are by size class III scorpions and size class IV scorpions have lower proportion of caterpillar prey and all other prey types as well in January–April. Size class III scorpions capture and consume a higher proportion of caterpillars during January–April perhaps because size class III scorpions are actively foraging in vegetation and utilizing microhabitats with more caterpillars available (McReynolds, in prep.) and size class IV scorpions are not very active and thus capture fewer caterpillars early in the year. One possible explanation for this difference in foraging success is that larger *C. vittatus* cannot climb as far out in the foliage where branches are thinner and more caterpillars are available. However, size class IV scorpions do capture a high proportion of caterpillars and other prey during September–December. Another possibility is that size class IV scorpions are not as active early because of temperatures below optimal early in the season while size class III scorpions are active even though temperatures are sub-optimal. This is supported by the low proportion of size class IV scorpions active during January–April and high proportion of size class III scorpions. Differences in locomotor ability among adults and juveniles and males and females (Carlson et al., 2014) could explain these differences in frequency of foraging and climbing during different time periods. The lower proportion of caterpillars captured during May–August by size classes II and III can be indication of low prey availability during this time period. Even though, a higher proportion of caterpillars are captured by size class IV scorpions during May–August than other size classes.

The activity and foraging success of different size classes of scorpions differ with four month time periods. One expected result from previous studies of *C. vittatus* is reduced activity during summer months (McReynolds, 2004, 2012), but this reduced activity during May–August only occurs for size class II and III scorpions. The peak activity for the different size classes can reflect differences in growth and behavior in the life history of *C. vittatus* (see Polis & Sissom, 1990). The high frequency of size class I scorpions in September–December could be due to many first instar scorpions leaving the dorsal mesosoma of their mother during August through October after molting to second instar (the second instar would be included in size class I scorpions). The high activity of size class IV scorpions in May–August could be due to increase search for mates by males, more courtship during this period, but perhaps the most important reason is increasing foraging by adult female scorpions to invest in reproduction even though foraging success can be low with lower prey availability. The metabolic requirements for the development of the embryos in the female *C. vittatus* could necessitate higher activity and foraging during May–August even if foraging success will be low (Formanowicz & Shaffer, 1993).

Foraging success of *S. mesaensis* is associated with prey availability and peaked in June (Polis, 1979). For *C. vittatus,* foraging success peaked during January–April then September-December but foraging success was not significantly different among time periods. However, foraging success varied with size of the scorpion and time period. Therefore, foraging success for *C. vittatus* does not just depend on prey availability alone. One possible factor for the variation in foraging success is that the activity of adult male and female (size class IV) scorpions are not just foraging while the other size classes would only be active when foraging. Adult scorpions can be searching for a mate (searching for a mate and prey are not necessarily mutually exclusive), courting or carrying young. Courting by *C. vittatus* has been observed during April through October with peaks in May and June and females carrying young have been observed in May through October with peaks in August and September (pers. obs.). This could reduce the foraging success of size class IV scorpions all year including the very low foraging success in January-April.

The temporal differences in activity and foraging success is determined by the risk of cannibalism for many species (Hallander, 1970; Polis, 1988a; Wagner and Wise, 1997; Rudolf, 2007; Rudolf & Armstrong, 2008). One hypothesis is that individuals with higher risk of predation (including cannibalism) will trade-off foraging success to reduce predation risk by using a sub-optimal habitat or time periods (Mittelbach, 1984; Werner & Hall, 1988; Morse, 2007). It is predicted that the larger more cannibalistic individuals will be active at the optimal time and with higher foraging success and smaller individuals will be active in sub-optimal times at the cost of lowering foraging success (trade-off) (Murdoch & Sih, 1978; Sih, 1981, 1982; Wissinger et al., 2010). In *S. mesaensis,* intraguild predation can cause a shift in habitat from the optimal sand dunes to the hard pan and sub-optimal time periods when larger scorpions are not active (Polis & McCormick, 1987). Size class IV scorpions show high activity in September-December (and May-August) time period and high foraging success with highest proportion of scorpions with prey in September-December. If January–April is a sub-optimal time period for scorpions, then this can explain why

Planned Comparisons	*G*	*df*	*P*
Caterpillar versus All Other Prey	13.956	2	< 0.001
Orthopteran and Intraguild Prey versus Moth and Other Prey	9.085	2	< 0.01
Orthopteran versus Intraguild Prey	1.51	2	ns
Moth versus Other Prey	3.506	2	ns
Total	**28.098**	**8**	**< 0.001**

Table 1: Planned comparisons among prey types of the contingency table for prey types versus scorpion size classes. All scorpions with prey except caterpillar prey (all other prey) were pooled for the first comparison versus scorpions with caterpillar prey. Then scorpions with orthopterans and intraguild prey were pooled for the second comparison versus scorpions with adult moth and other prey pooled. The third comparison was scorpions with intraguild prey versus scorpions with orthopteran prey. The last comparison was moths versus other prey. ns = not significant, see Figure 3.

Planned Comparisons	*G*	*df*	*P*
Caterpillar versus All Other Prey	28.843	2	< 0.001
Orthopteran and Intraguild Prey versus Moth and Other Prey	1.385	2	ns
Orthopteran versus Intraguild Prey	0.083	2	ns
Moth versus Other Prey	6.315	2	< 0.05
Total	**36.596**	**8**	**< 0.001**

Table 2: Planned comparisons among prey types of the contingency table for prey types versus months of the year. All scorpions with prey except caterpillar prey (all other prey) were pooled for the first comparison versus scorpions with caterpillar prey. Then scorpions with orthopterans and intraguild prey were pooled for the second comparison versus scorpions with adult moth and other prey pooled. The third comparison was scorpions with orthopteran prey versus scorpions with intraguild prey. The last comparison was moths versus other prey. ns = not significant, sSee Figure 4.

Comparisons	*G*	*df*	*P*
Interaction	6.224	8	ns
Conditional			
Prey Type versus Months of the Year	29.682	12	< 0.01
Size Class versus Prey Type	16.699	12	ns
Size Class versus Months of the Year	41.808	12	< 0.001

Table 3: Three-way G test of independence of the contingency table for prey types versus months of the year versus scorpion size classes. ns = not significant. See Figure 5.

Comparisons	*G*	*df*	*P*
Interaction	14.859	4	< 0.01
Conditional			
Prey Type versus Months of the Year	16.482	6	< 0.05
Size Class versus Prey Type	36,692	6	< 0.001
Size Class versus Months of the Year	516.68	8	< 0.001

Table 4: Three-way G test of independence of the contingency table for scorpions with prey or no prey types versus months of the year versus scorpion size classes, see Figure 8.

the size class IV scorpions show low activity and low foraging success during this time period. Size class III scorpions high activity in January–April and having lower activity (lowest for size class III during May–August) when size class IV scorpions are more active fits the predicted pattern. However, the foraging success of size class III scorpions and activity of size class I and II scorpions do not fit the predicted pattern of a trade-off to avoid larger cannibalistic individuals. Foraging success by the intermediate size scorpions (size class III) during January–April does not appear to be a trade-off to avoid cannibalism because size class III scorpions capture the highest proportion of prey (especially caterpillars) during this time period. In addition, smaller scorpions (size class I, II and III scorpions) have high active during September–December but not as high as size class IV scorpions.

More likely explanation is that prey availability of different prey types vary with time period, and efficacy of foraging methods vary with ontogeny. The possibility is that seasonal variation in availability of different prey types leads to differences in effectiveness of foraging methods at different time periods. For example, if size class III scorpions are more efficient at active search and climbing in search of prey such as caterpillars, then high availability of caterpillars in March and April because of high precipitation (Quintanilla, 2008) and new foliage can lead to more caterpillars captured during the January–April time period by size class III scorpions and high foraging success overall. On the other hand, if there is a high availability of orthopteran and intraguild prey during September-December, then ambush (sit-and-wait) foraging by size class IV scorpions can be more successful than for other size classes because the larger scorpions can handle these more dangerous and difficult prey. This can explain the significant interaction on the three-way G test (Table 4) because activity and foraging success by the different size classes shifted with the type of prey available during different time periods.

The prey items described in this study do not include all prey captured. The reasons for this include: (1) Scorpions carrying prey to a refuge instead of feeding where captured or carrying prey into vegetation. Scorpions can find a refuge nearby in holes in the ground including wolf spider burrows or under dense vegetation and leaf litter. (2) Some prey are quickly handled and consumed thus a short handling time. Observations of these prey items are less likely because the prey are captured and consumed at the capture site. If termites and ants for example have a short handling time then ants and termites would rarely be observed as prey (only one of each observed of the 304 prey) even though both are abundant and scorpions have been observed near ant nests and trails and termite tubes (pers. obs.). (3) Small prey are not always observed in the field or prey dropped before being observed and identified. (4) Prey captured later in the night are less likely to be observed because observations of scorpions rarely went past midnight and no later than 2 AM.

Further study is needed to address a number of questions raised by this study.Are caterpillars the preferred prey by all *C. vittatus* in South Texas? Are caterpillars high in nutritional value and low toxin levels for scorpions thus a preferred prey? Alternately, do caterpillars have low nutritional value or high toxin levels for scorpions and thus are sub-optimal prey with high predation rate because of high availability? When do scorpions actively forage for prey versus forage by ambush (sit-and-wait)? What effect does prey availability of different types of prey (e.g., caterpillars) have on foraging methods and success? Is *C. vittatus* climbing into different species of vegetation just to feed, ambush prey such as moths or climb in vegetation to search for prey such as caterpillars (McReynolds in prep.)? Is the temporal differences in activity and foraging success of different size classes of *C. vittatus* because of efficacy of foraging method, seasonal differences in prey availability or tradeoffs because of predation risk including cannibalism? The case for a tradeoff due to cannibalism does not have support unless caterpillars are sub optimal prey with low nutritional value for scorpions. Does the effectiveness of different foraging methods and the type of prey captured for different size scorpions involve climbing ability, venom potency and/or size of pedipalps and stinger? In addition, how do scorpions handle captured prey? Do *C. vittatus* mainly feed in vegetation or do some scorpions (including size class I scorpions) often handle prey by carrying the prey into a refuge? What is the function of feeding on prey in vegetation? Is it to more effectively handle prey or is it avoid predators and interference while feeding?

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