2022. Journal of Arachnology 50:267–276

Vinegaroons (Uropygi: *Mastigoproctus tohono*) in a multi-predator/multi-prey system: Prey, predators, and cannibalism

Justin O. Schmidt and **Li S. Schmidt**: Southwestern Biological Institute, 1961 W. Brichta Dr., Tucson, AZ 85745, USA; E-mail: ponerine@dakotacom.net

Abstract. Vinegaroons are members of a guild of apex arthropod predators in the high desert grasslands of southeastern Arizona. Despite their importance as major predators in the ecosystem, almost nothing is known about their potential prey, predators, or competitors. We evaluated predator-prey relationships of vinegaroons and 30 species of potential prey, 27 species of potential predators, and the detailed interactions among three taxa of their apex predator guild. With few exceptions, vinegaroons overpowered and preyed on most potential prey within a suitable size range, were almost immune to predation, and appeared to be the dominant species in interactions with other predator guild members. Their most vulnerable life stages were the first two free-living instar stages, whereas adults and fourth instar individuals were not preyed on by any predators active in the same areas and times as vinegaroons. Third instar individuals were a crucial transition stage in which they had a few predators but also were large enough that they required capturing many prey items to grow sufficiently to molt to the fourth instar. In interactions among arthropod predators, the general observation was that when predation occurred, the larger individual usually prevailed irrespective of taxon. Cannibalism among adult and fourth instar vinegaroons does not occur under natural conditions in contrast to when they are placed together in artificial stressful situations. Cannibalism of the three smallest instars appears likely and might partially explain why they are solitary and spend minimal time foraging.

Keywords: Whipscorpion, *giganteus*, Thelyphonida, Thelyphonidae, predator guild

https://doi.org/10.1636/JoA-S-21-005

Vinegaroons are invertebrate predators found in many different tropical regions of the world, including America, Asia and West Africa (Harvey 2003). *Mastigoproctus tohono* Barrales-Alcalá, Francke & Prendini, 2018, occurs throughout southeastern Arizona, USA and northeastern Sonora, Mexico (Barrales-Alcalá et al. 2018). They are ambush predators that tend to move slowly and spend much time waiting for prey to come nearby, at which time they rapidly rush and grab the prey with their pedipalps (Schmidt 2009). Other significant invertebrate predators in the environment include the large spiders *Aphonopelma* Pocock, 1901 sp. and *Hogna carolinensis* (Walckenaer, 1805), scolopendrid centipedes (*Scolopendra polymorpha* Wood, 1861), sun spiders (Solifugae spp.), scorpions (Scorpiones spp.), and large carabid ground beetles (*Calosoma* spp.). Although vinegaroons are commonly called whipscorpions, they lack a sting apparatus like their scorpion relatives. Nevertheless, they can be dangerous prey that defend themselves with their large pedipalps and their ability to spray highly concentrated acetic acid admixed with other aliphatic acids (Eisner et al. 1961; Yogi & Haupt 1977; Itokawa et al. 1981, 1985; Haupt et al. 1988, 1993; Schmidt et al. 2000; Haupt & Müller 2004). Their common name "vinegaroon" is derived from their ability to spray this toxic vinegary-smelling mixture (Figure 1).

Prey animals are usually under selection pressure from multiple predators (Brodie & Brodie 1999). Examples include ungulate prey and their predators in Africa (Thaker et al. 2011; Creel et al. 2017), invertebrate inhabitants of temporary ponds that lack fish (Klecka & Boukal 2012), and birds preying on frogs (Willink et al. 2014). A variety of studies explore scenarios involving two species of predators and one of prey. Examples come from a wide range of taxa including shorebirds with two avian predators (Cresswell & Quinn 2013), tadpoles with fish and dragonfly naiad predators (Eklöv 2000) or tadpoles with salamanders and dragonfly naiads (Kishida & Nishimura 2005), roaches with two other fish species (Martin et al. 2010), mayflies with stoneflies and trout (McIntosh & Peckarsky 1999), deer with lynx and humans (Lone et al. 2017), and tiger moths with birds and bats (Ratcliffe & Nydam 2008). Intraguild predation among predators has also been a focus among a diversity of predators including spiders (Finke & Denno 2002), crabs (Grabowski et al. 2008), coccinellid beetles and other predators (Weber & Lundgren 2009), owls, weasels and voles (Hoset et al. 2009), and has been reviewed by Polis et al. (1989) and Michalko et al. (2019).

Dangerous prey present a special situation for predators (Mukherjee & Heithaus 2013). Vinegaroons are considered dangerous prey for several reasons, including their defensive spraying of toxic fatty acids on predators and their ability to "turn the tables" by becoming the predator. Vinegaroons are also members of a guild of large arthropod predators and thus present an opportunity to document interactions both within and outside this guild.

Mastigoproctus tohono is a recently described member of the *giganteus* species group (Barrales-Alcalá et al. 2018), which contains the largest-sized members in the order Uropygi. Vinegaroons are usually considered to be generalist predators that accept most any potential prey within the size range that they can overpower. Few investigations have focused on their choice of prey and most reports documented their feeding on unusual prey, such as amphibian eggs (Toledo 2007), conspecifics (Armas & Rivera 2009), millipedes (Carrel & Britt 2009), or dung beetles (Noriega & Botero-Trujillo 2008). Predators of vinegaroons have received limited attention, mainly examinations of predatory rodents attacking adult

Figure 1.—A vinegaroon spraying its acid containing chemical defense on a threatening attacker (forceps). Photograph courtesy of Bruce D. Taulbert.

vinegaroons (Eisner et al. 1961) and free-living first instar nymphs avoiding the odor of large wolf spiders (Punzo 2005). This paucity of knowledge is partly because vinegaroons are strictly nocturnal creatures that do not fluoresce like scorpions, are not attracted to lights, are dark colored, and are slow moving, making them difficult to study. We report here on field observations and laboratory experiments to determine the breadth of prey that vinegaroons accept, what predators they are likely to encounter, and how various sizes of immatures and adults might behave to minimize risks of predation or cannibalism.

METHODS

Animals.—Free-ranging individuals of *Mastigoproctus tohono* were captured by hand at night during systematic transit surveys where they were spotted in the light of observer headlamps while on the soil surface. The survey plot was a square 160 m on edge and consisted of old, mostly flat or gently sloping stabilized and weathered sandy-loam dunes near Willcox, Cochise County, Arizona (32°14′16″N, 109°46′15″W; 1,279 m asl [above sea level]). Collections were performed in the years between 1988 and 1998 during the summer rainy season beginning in July and continuing into early autumn. During the more than 500 hours of surveys in the field by the authors, any vinegaroons with prey were captured and the prey removed for identification, if possible. Captured adult and fourth instar vinegaroons were maintained in captivity in 4-liter jars of 15 cm diameter x 24 cm high filled to a height of 16 cm with moistened sandy-loam soil taken from the survey plot. First through third instar vinegaroons were maintained in the same condition as adults, except in correspondingly smaller jars. The laboratory temperature ranged from 24–32°C with a relative humidity range from 30–60%. The animals were fed a variety of insects mostly captured at blacklights during the dark hours, or on the ground during daylight in the Willcox study area or in Tucson, Arizona. The prey consisted mainly of cockroaches, beetles, caterpillars and crickets. The jars were capped with lids fitted with screened central holes to provide limited ventilation. Many of the younger instars were bred in the laboratory from adults previously captured at the study area (Schmidt et al. 2021).

Laboratory predator-prey tests.—Various categories of potential prey were evaluated to determine if they were acceptable to vinegaroons of different immature instars and adults. The categories included: generally expected to be palatable prey that lacked strong mechanical, chemical or venomous defenses; mechanically defended insects that have dense setae or hardened integuments; chemically defended species that possess known chemical defenses, including some that have internal toxins; venomous species that can deliver venoms through either a sting or a bite; and a final category of prey that were observed being eaten in the field by a vinegaroon (Table 1). As much as possible, tested prey

Table 1.—Potential prey of vinegaroons of various developmental stages.

Prey	Common name	*n*[a]	Vinegaroon stage	Result[b]	Comment
GENERALLY PALATABLE PREY					
Stagmomantis limbata	Praying mantis	1	Adult	+	Small immature
Hydrophilidae sp.	Aquatic beetle	3	Adult	3+	
Cicindela sp.	Tiger beetle	1	Adult	+	
Acromyrmex versicolor	Leafcutter ant	1	Adult	+	Alate female
MECHANICALLY DEFENDED PREY					
Pyrrharctia sp.	Woolly bear	2	Adult	1+;1-	Caterpillars
Hemiphileurus illatus	Armored beetle	2	Adult	2-	
H. illatus		4	4th	4-	
H. illatus		3	3rd	-	
NOXIOUS CHEMICALLY DEFENDED PREY					
Myrmeleontidae sp.	Ant lion adult	1	Adult	+	
M. sp.		2	3rd	2+	
Chrysomelidae sp.	Leaf beetle	5	Adult	5+	Each ate 2 beetles
Tegrodera erosa	Blister beetle	12	Adult	8+;4-	11 beetles eaten
T. erosa		2	4th	2-	1 killed but not eaten
T. erosa		1	3rd	-	Killed but not eaten
Pyrota akhurstiana	Blister beetle	13	Adult	12+;1-	
Eleodes sp.	Stink beetle	3	Adult	1+;2-	
Brachinus elonatulus	Bombardier	1	Adult	+	3 beetles eaten
Battus philenor	Pipevine	2	Adult	2-	Caterpillar probed, not eaten
Taeniopoda eques	Horse lubber	1	Adult	+	Last instar hopper
T. eques		2	4th	2+	Last instar hoppers
Dinothrombium sp.	Giant velvet mite	20	Adult	1+;19-	1 killed, not eaten
D. sp.		9	4th	9-	
PREY WITH VENOMOUS STINGS OR BITES					
Dasymutilla bioculata	Velvet ant	5	Adult	3+;7-	Two tests on separate days
D. foxi		1	Adult	+	Regurgitation killed, eaten
D. chiron		2	Adult	2-	
D. gloriosa		2	Adult	2-	
Pogonomyrmex rugosus	Harvester ant	1	Adult	+	Ate 4 ants
P. rugosus		1	3rd	+	Ate 2 ants
P. rugosus		9	2nd	8+;1-	Ate total of 36 ants
P. maricopa	Harvester ant	4	4th	3+;1-	
P. maricopa		3	3rd	3+	Each ate 3 ants
P. maricopa		1	3rd	+	Ate 17, 18th stung and killed
P. maricopa		1	2nd	+	
P. maricopa		1	1st	-	Stung, killed by ant
Pepsis sp. male	Tarantula hawk	1	Adult	-	
Pepsis sp. male + female		1	Adult	+	Ate 2 males, not female
Lethocerus sp.	Giant water bug	2	Adult	2-	
Chihuahuanus russelli	Scorpion	1	Adult	+	
C. russelli		2	3rd	2-	
FIELD OBSERVATIONS					
Elateridae sp.	Click beetle	1	Adult	+	
Phyllophaga sp.	June beetle	1	3	+	
Solpugidae sp.	Sun spider	1	Adult	+	Large sun spider
Chihuahuanus russelli	Scorpion	1	4	+	

[a] *n* = the number of different individual vinegaroons tested.

[b] + = prey was eaten; - = prey was not eaten.

animals were taken from the same habitat as the vinegaroons, or from nearby areas in southern Arizona.

Laboratory tests were conducted in a series of arenas ranging in size from 16 × 30 cm to 36 × 60 cm, depending upon the sizes of the animals involved. Soil from the original habitat of the vinegaroons was used to cover the surface of the arenas. The tests were conducted by introducing the potential prey into the arena that already contained the vinegaroon. In most cases, the interactions were observed until the prey was captured, or the two had interacted and thereafter avoided each other. In some exceptional situations, the animals were left together for 24 hours and scored at the end. These longer-lasting experiments were usually performed in the case of the prey exhibiting escape behavior such that the vinegaroon was unable to capture it within one hour. In tests where the potential prey was not attacked, a palatable prey item was offered, and if eaten the test was considered valid. If the prey was not eaten, the trial was eliminated.

The same general procedures were followed for testing potential predators of vinegaroons, with the exception that the vinegaroon was added to the arena already containing the potential predators. In some cases, different sized predators and/or different instars of vinegaroons were tested to determine if size might be an important factor governing the interaction.

Permits beyond an Arizona hunting license were not required before year 2005 for any of the vertebrate potential predators, including the box turtles that were tested (https://www.azgfd.com/hunting/regulations/; downloadable PDF under Arizona Reptile and Amphibian Regulations). The box turtles were released within a week of capture back into the Willcox study site at the exact location where they were originally found.

Cannibalism.—Oval enclosures measuring 2 × 2.7 m were constructed in the field at locations where vinegaroons were abundant. Each enclosure consisted of sides constructed of 0.4 m wide galvanized steel flashing that was driven 10 cm into the soil; the top was open to allow natural field conditions to be maintained. The vegetation within the enclosures consisted mainly of sparse grass and small burroweeds (*Isocoma tenuisecta*) and was undisturbed except to trim areas touching the surrounding flashing to prevent escape. The sides of the flashing were too slippery to be climbed by the vinegaroons. The authors had noted in earlier studies that vinegaroons did not exhibit unnatural or escape behaviors when subjected to red light (Schmidt et al. 2021) but did react photo-negatively to incandescent light (Patten 1917). For this reason, we assumed that vinegaroon behavior was not affected by red light and used a red light (F40R, General Electric, Boston, MA, USA) suspended 1.5 m above each enclosure to visualize their activities.

Various numbers and sizes of vinegaroons were added to the enclosures shortly after sunset and the individual activities were monitored periodically throughout the night. Just before sunrise, all individuals were removed, and any damage or death of an individual was recorded. On three occasions, recently killed individuals were added to the enclosures to determine if those individuals would be scavenged and cannibalized. All observations were performed in the active summer wet season during conditions when individuals would be naturally active.

RESULTS

Potential prey.—Results of potential prey encounters with vinegaroons are recorded in Table 1. The first group presented to vinegaroons were of prey that would be generally considered palatable because of their lack of strong defenses. These prey consisted of a praying mantis, three large aquatic beetles, a tiger beetle, and a winged female ant. All individuals were readily eaten except legs and some pieces of the hard integument of beetles, something that indicates their general acceptability to the adult vinegaroons.

The next group of prey consisted of species that have mechanical defenses. These were fed to adult and third and fourth instar vinegaroons and included large hairy caterpillars and large heavily armored beetles. One caterpillar was eaten, the other was not. The beetles were too hard for the vinegaroons to penetrate and thus were successful in avoiding predation.

A large grouping of chemically defended prey were presented and yielded mixed results. Antlions and leaf beetles were consumed, as were some blister beetles, and one of three *Eleodes* stink beetles. Bombardier beetles and horse lubber grasshoppers were eaten, whereas both pipevine swallowtail caterpillars were unharmed and of the 29 giant velvet mites offered, only one was killed, and it was not eaten.

Many species of prey were presented that possessed venomous stings or bites, including four species of velvet ants, two species of harvester ants, tarantula hawk wasps, and giant water bugs. The velvet ants are defended by both hard integuments and painful stings (Schmidt & Blum 1977). We cannot determine which property, or if both were important in protecting most velvet ants from predation. In one case after struggling with the velvet ant for some time, the vinegaroon regurgitated a sticky liquid that covered the velvet ant, killing it. It was subsequently consumed. Vinegaroons of all immature life stages were challenged with the venomous stinging harvester ants. The ants were acceptable to all the immature vinegaroons, though with some risk of being bitten (Figure 2A) or stung. Two vinegaroons, one 3rd instar and one 1st instar, were stung by ants through the membranes of their pedipalp joints, and thereby killed (Figure 2B,C). Two male tarantula hawks were consumed, but not a tested female. Likewise, the giant water bugs were ignored. A scorpion was attacked and consumed by an adult vinegaroon, but two smaller 3rd instar vinegaroons avoided the scorpions.

A final group of prey consisted of those that were recorded in the field as they were being consumed by vinegaroons. These included a click beetle, a June beetle, a sun spider, and a scorpion being eaten telson first. Other unidentified prey were also observed (Figure 2D).

Potential predators.—Potential predators of vinegaroons were tested in the laboratory arenas (Table 2). The first category of potential predators consisted of vertebrate species that are present in the same environment as the vinegaroons. Five of the nine box turtles succeeded in eating vinegaroon adults or later instar immatures. Commonly, the turtle would attempt to immobilize the vinegaroon by stepping upon it, often resulting in getting sprayed in the eye. In response, several turtles discontinued the attack and did not attack again. Other turtles endured the apparent pain of being sprayed and, nevertheless, persisted and ate the vinegaroon. Four local snakes from the habitat were tested, none of which exhibited any interest in the vinegaroons. Of the seven species of lizards, only one tree lizard and one spiny lizard preyed on the small 1st instar vinegaroons they were offered; the rest looked at the vinegaroons and either ignored them or licked and then ignored them. Four great plains toads were tested and only one large 65 g individual ate three 1st instars before refusing all others afterwards. Of 11 challenged individual spadefoot toads, only one 1st instar vinegaroon was eaten and that spadefoot did not subsequently attack other vinegaroons.

Arachnid potential predators of vinegaroons were common in the habitat and included tarantulas, scorpions, and sun spiders. In general, the adult female tarantulas preyed on the smaller vinegaroons (3rd instar and earlier) but avoided adult and 4th instar vinegaroons. The smaller species of scorpions avoided the three earliest instars of vinegaroons. Adults of the midsized *Paravaejovis spinigerus* (Wood, 1863) revealed a

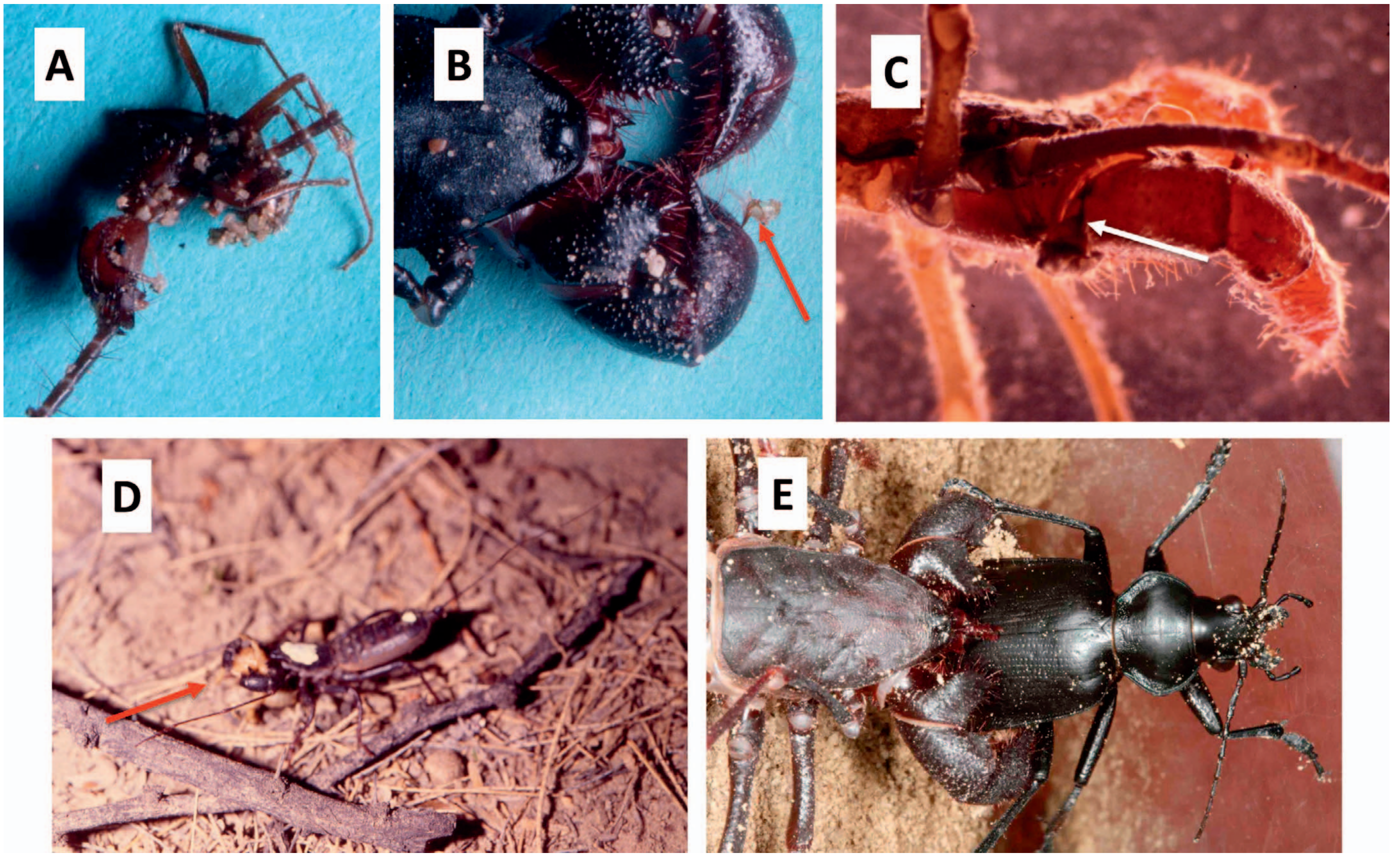

Figure 2.—Vinegaroons in captivity and in the field with different prey items. (A) A still-attached dead harvester ant, *Pogonomyrmex maricopa*, that had bitten and severed the tail of a vinegaroon. (B) Autotomized stinger of a *Pogonomyrmex maricopa* (red arrow) remaining attached in the intersegmental membrane of the pedipalp of a 3rd instar vinegaroon that was killed by the sting. (C) Autotomized stinger of a *Pogonomyrmex maricopa* (white arrow) remaining attached in the intersegmental membrane of the pedipalp of a 1st instar vinegaroon that was killed by the sting. (D) A vinegaroon consuming an unidentified prey (red arrow) in the study site. (E) A vinegaroon attempting to penetrate the hard exoskeleton of a beetle, *Calosoma* sp. Vinegaroons often held these beetles for several hours while attempting to subdue them before finally succeeding.

mixed picture. Of the three individuals tested, one scorpion and vinegaroon avoided each other, one scorpion ate the 3rd instar vinegaroon, and one 3rd instar ate the scorpion. The large scorpions, *Hadrurus arizonensis* Ewing, 1928*,* consumed all 2nd and 3rd instar vinegaroons they were provided but the one individual given a 4th instar resulted in a mutual avoidance. Sun spiders, though extremely fast voracious predators, appeared not to be a threat to even the smallest vinegaroons. In contrast, one 2nd instar vinegaroon captured and ate a sun spider.

Two species of potential insect predators—large praying mantises and large predacious ground beetles—were tested with 1st instars. Only the one huge female mantis attacked and consumed the much smaller vinegaroon; none of the smaller male mantises or five ground beetles preyed on 1st instar vinegaroons.

Dynamic predator-prey intraguild relationships.—A guild of several large arthropod predators co-inhabit the study site with vinegaroons and are active at the same times during the night. We focused attention on three common species that might be both predators and prey of vinegaroons. *Hogna carolinensis* is the largest wolf spider in the habitat and presents serious risks to both 1st and 2nd instar vinegaroons (Table 3). Third instar vinegaroons are equal in weight or greater than adult *H. carolinensis*, resulting in mixed predation. Only one of eight tested vinegaroons was overwhelmed and eaten by a spider. In a test with a smaller immature spider, the 3rd instar vinegaroon prevailed. The largest vinegaroons, 4th instars and adults, became predators of the spiders. Giant centipedes, though much larger than small vinegaroons, only rarely attacked and preyed on the vinegaroons. No large (4th instar or adult) vinegaroons were attacked and the tables were turned, in which adult vinegaroons often preyed on the centipedes. *Calosoma* sp. is an abundant, large predacious beetle that is both quick and voracious. In only one of 29 challenges involving 1st or 2nd instar vinegaroons was the vinegaroon overwhelmed and eaten. In contrast, in almost all encounters pairing large vinegaroons, the beetle was eaten. This was despite the beetles being protected by both chemical defenses and having hard exoskeletons. The vinegaroons often held the beetles and struggled for several hours before succeeding in penetrating the beetles' integument with their chelicerae (Figure 2E).

Cannibalism.—Various numbers and life stages of vinegaroons were added to open-air enclosures placed in their natural environment where they were living (Table 4). The

Table 2.—Potential predators of vinegaroons of various developmental stages.

Potential predator	Common name	*n*[a]	Vinegaroon stage	Result[b]	Comment
Vertebrates					
Terrapene ornata	Box turtle	5	Adult	2+;3-	Stepped on to restrain
T. ornata		2	4th	1+;1-	
T. ornata		2	3rd	2+	
Arizona elegans	Glossy snake	1	Adult	-	
Heterodon nasicus	Hognosed snake	1	Adult	-	
Rhinocheilus lecontei	Longnose snake	2	Adult	-	
R. lecontei		1	2nd	-	4.56 g snake
Lampropeltus getula	King snake	2	Adult	2-	
Aspidocelis tigris	Whiptail lizard	1	1st	-	Licked and rejected
Urosaurus ornatus	Tree lizard	4	1st	1+;3-	
Sceloporus undulatus	East fence lizard	1	1st	-	
S. occidentalis	West fence lizard	3	1st	3-	
S. magister	Spiny lizard	1	1st	+	Ate 3 individuals
S. jarrovii	Spiny lizard	1	2nd	-	3.17 g lizard
Phrynosoma cornutum	Horned lizard	1	1st	-	Ate many *Pogonomyrmex*
Bufo cognatus (large)	Great plains toad	1	Adult	-	
B. cognatus		1	3rd	-	
B. cognatus		1	2nd	-	
B. cognatus		1	1st	+/-	64.8 g; ate 3, refused others
Scaphiopus couchii	Couch spadefoot	1	4th	-	
S. couchii		1	2nd	-	
S. couchii		4	1st	1+; 3-	1 eaten, none thereafter
Spea bombifrons	Plains spadefoot	5	1st	5-	
Spiders					
Aphonopelma chalcodes Chamberlin, 1940	Tarantula	1	4th	-	Avoided each other
A. chalcodes		5	3rd	5+	
A. chalcodes		2	1st	2+	
Scorpions					
Chihuahuanus russelli (Williams, 1971)	Russells scorpion	2	1st	2-	
C. russelli		1	2nd	-	
C. russelli		3	3rd	3-	
C. russelli		1	Adult	-	Scorpion was eaten
Paravaejovis spinigerus (Wood, 1863)	Scorpion	3	3rd	+/-	1 3rd eaten; 1 scorpion eaten
Centruroides sp.	Bark scorpion	1	3rd	-	
Hadrurus arizonensis Ewing, 1928	Giant hairy scorpion	5	2nd	5+	
H. arizonensis		9	3rd	7+;2-	
H. arizonensis		1	4th	-	
Sun spiders					
Solpugidae sp.	Sun spider	1	1st	-	
Solpugidae sp.		2	2nd	2-	Solpugid was eaten
Insects					
Stagmomantis limbata	Praying mantis	1	1st	+	Large female mantis
S. limbata		2	1st	2-	Male mantises
Scarites sp.	Big-head carabid	5	1st	5-	

[a] n = number of different individual predators tested.

[b] + = vinegaroon eaten; - = vinegaroon not injured or eaten.

earliest tests with one male and one female, or with two or three males alone resulted in no deaths or injuries. Next, various combinations of males and females were placed in the arenas along with fourth instar individuals. Again, no deaths or injuries were observed and in one case a pair was observed mating within the enclosure. At this point, larger numbers of individuals consisting of males, fourth instars, and third instars were combined. In two tests involving third instars in arenas with two males and one fourth instar, the third instar vinegaroons survived, though sometimes they climbed into the burroweeds for safety. In each of two other tests with third instars, a male was observed killing and cannibalizing a third instar. No fourth instars were observed eating another individual in any of these tests.

To determine if scavenging/cannibalism was engaged in opportunistically, three tests involving recently killed individuals (one by physical damage and two by freezing) revealed no scavenging or feeding on the dead individuals. This was despite as many as nine or 11 individuals in the enclosure with the dead individual. In several instances, a living individual touched the dead individual with its antenniform legs and then walked away.

Over 98 individual-nights, only two cases of cannibalism were observed, and both involved adults preying on much smaller third instar individuals. This was despite the density of

Table 3.—Intraguild predator-prey relationships involving vinegaroons.

Potential predator/ prey	Common name	*n*[a]	Vinegaroon stage	Results and comments: (V= vinegaroons; **bold** when the vinegaroon was the predator)
SPIDERS				
Hogna carolinensis (Walckenaer, 1805)				
H. carolinensis	Wolf spider	3	1st	All 3 V were eaten
H. carolinensis		2	2nd	Both V were eaten
H. carolinensis		8	3rd	Only 1 of 8 V was eaten
H. carolinensis		1	3rd	**The 0.246g spider was eaten**
H. carolinensis		3	4th	**2 of 3 spiders (1.27 and 1.96g) were eaten**
H. carolinensis		1	Adult	**Full -sized spider was eaten**
CENTIPEDES				
Scolopendra polymorpha	Giant centipede	3	1st	No predation (0.50-1.42g centipedes)
S. polymorpha		5	2nd	No predation
S. polymorpha		7	3rd	2 of 7 V were eaten
S. polymorpha		2	4th	No predation
S. Polymorpha		10	Adult	**6 of 10 centipedes (0.50-4.41g) were eaten**
INSECTS				
Calosoma sp.	Carabid beetle	21	1st	No predation
Calosoma sp.		8	2nd	1 of 8 V was eaten
Calosoma sp.		6	3rd	No predation
Calosoma sp.		16	4th	**13 of 16 beetles were eaten**
Calosoma sp.		19	Adult	**All 19 beetles were eaten**

[a] *n* = the number of different individuals of predator/prey tested.

individuals within the enclosures being many times greater than is ever observed naturally in the field. During a typical good all-night search about 10 individuals are observed (unpublished data).

DISCUSSION

Most predator-prey studies focus either on prey and how they adapt to and evade predation, or on predators and how they obtain prey. Less common are studies involving apex predators and other guild members and their prey. Few studies involve complex situations in which predators must deal with a diversity of prey species as well as their own predators (Schmidt & Blum 1977; Sherbrooke 2003). This investigation centered on an arachnid species in the middle of a complex suite of diverse prey, often present in low numbers, plus a multitude of their own potential predators.

Table 4.—Potential cannibalism in encounters of vinegaroons of various developmental stages.

Males (*n*)	Females (*n*)	4th instars (*n*)	3rd instars (*n*)	Total (*n*)[a]	Predated (*n*)[b]	Comments
1	1			2	-	
2				2	-	
3				3	-	
3				3	-	
2	1	2		5	-	
2		2		4	-	
2		2		4	-	
2		3		5	-	
3		3		6	-	
3		3		6	-	
3	1	3		7	-	
4	2	3		9	-	Pair mating
2		1	1	4	-	
2		2	1	5	1	Male eating 3rd at 04:15
2		1	2	5	-	
2		1	2	5	1	Male eating 3rd at 21:45
	Fresh, dead individual added					
1	1	1		3	-	Freshly killed male untouched
5		6		11	-	Freshly frozen male untouched
5	1	3		9	-	Freshly frozen male untouched

[a] Total number of individuals simultaneously in enclosure.

[b] - = No cannibalism or scavenging of a freshly killed individual.

Vinegaroons share the soil surface of the high desert grassland study site with a vast suite of potential prey, including many that are protected mechanically, chemically, with venomous stings or bites, or combinations of these. We intentionally focused on prey having these defenses to determine how broad the potential diet of vinegaroons is likely to be. In general, even prey with these defenses were often not sufficiently protected to deter predation by vinegaroons. For example, the extreme density of spines on woolly bear caterpillars did not offer complete protection against predation. In contrast, the extremely hard exoskeletons of *Hemiphileurus illatus* (Coleoptera: Scarabaeidae) were too hard for any of the vinegaroons to crush and in this case did confer protection. Many chemically defended prey were also vulnerable. In some chemically defended species (blister beetles and stink beetles), partial protection was afforded and in others (giant velvet mites) protection was essentially complete. Some prey species with chemical defenses (adult antlions, leaf beetles, blister beetles) avoided predation by remaining aboveground in the vegetation during the nighttime and therefore out of reach of vinegaroons. Giant velvet mites were doubly protected from vinegaroons by being both unpalatable and active on the soil surface only after sunrise, thus also being temporally separated from vinegaroons. The venoms of potential prey appeared not to confer much protection from predation by vinegaroons. Venomous velvet ants often survived attacks, but this may have been a result of their hard, impenetrable integument rather than their venom. Harvester ants presented a fascinating picture. Large numbers of them were preyed on by small vinegaroons but not without risk. They are risky prey that not only can bite, but in rare cases can also sting and kill vinegaroons. Large vinegaroons did not prey on harvester ants, but was this because they are not worth the effort, or because they are potentially dangerous? One answer could be that smaller vinegaroons would have more limited prey options and might be more willing to risk the hazard of handling harvester ants. Female tarantula hawks and giant water bugs were not attacked by vinegaroons, likely because they were too large, irrespective of their venom (the much smaller male tarantula hawks were grabbed and consumed). The scorpions in the study area are both venomous and dangerous prey, though they were smaller than fourth instar or adult vinegaroons, but larger than first or second instars. Adult vinegaroons readily preyed on scorpions, whereas scorpions and the third and smaller instar vinegaroons avoided each other.

Few potential predators were observed to prey on vinegaroons and those that did mostly preyed on the smaller instars. Vertebrate potential predators, though in the habitat and often considerably larger than vinegaroons, rarely preyed on them. For adult vinegaroons, the only species that successfully preyed on them were box turtles, but even then, only sometimes. This potential predation by box turtles is likely irrelevant in the field and artificial because the two species do not overlap temporally; box turtles are only active during the day and vinegaroons only at night. Even the small first and second instar vinegaroons were generally avoided by all test vertebrate predators present in the area. The rare exceptions involving predation on first instars by lizards are, likewise, not ecologically relevant because the lizards are active during the day and vinegaroons only at night. Toads and spadefoots are abundant and active at night in the study area. They might be major predators of first instar vinegaroons simply because of their sheer numbers. Nevertheless, they might not be an overwhelming threat because individuals that had experienced a previous encounter with vinegaroons might avoid them. Arthropod predators are abundant in the area, and many are active during the same times as vinegaroons. Despite overlapping physically and temporally with vinegaroons, arthropod predators were not generally a large threat. The only exceptions were adult tarantulas found in low numbers in the habitat. They were a threat to the first three instars of vinegaroons. In an extreme test situation with scorpions, giant hairy scorpions were found to prey readily on the first three instars of vinegaroons, though not on a fourth instar during the one opportunity presented. Again, this predation would be irrelevant in the studied environment because those scorpions are not present in or near the environment. This species was included because we felt that their ranges might overlap in other areas.

Of special interest for elucidating weak links in the life table of vinegaroons was the question of intraguild predation and competition among the large abundant arthropod predators in the vinegaroon habitat. These guild members included the large ambush wolf spiders (*Hogna carolinensis*), giant cursorial centipedes (*Scolopendra polymorpha*), and the largest of the ground beetles (*Calosoma* sp.). These apex predators were paired with all stages of vinegaroons to determine who preys on whom, and when. None of the first or second instar vinegaroons preyed on their potential predators, whereas both the spiders and the ground beetles sometimes preyed on them. An apparently crucial stage in the life of vinegaroons is their third instar stage. They are large enough that they need to capture quantities of prey to gain sufficient weight to molt to the fourth instar (Schmidt et al. 2021), yet they need to avoid their own predators. The dynamic played out that sometimes third instars were preyed on by the wolf spiders and centipedes and sometimes they preyed on the spiders (but not the centipedes or beetles). By the time the vinegaroons became fourth instars, they were sufficiently large that they regularly preyed on the spiders and beetles and were never prey of any of the predators. Adult vinegaroons then became predators of all three of the other predators. Within this guild of apex predators, the general rule emerged that, in predatory encounters, the larger individual usually prevailed. This also explains the observations that first and second instar vinegaroons are almost never seen in the field (Punzo 2000; unpublished data) and third instars are rarely observed. This also suggests that the weakest links in the life history of *Mastigoproctus tohono* are the two youngest instars in their lives.

Final potential predators of vinegaroons are conspecifics that might engage in cannibalism. Among biologists, cannibalism within vinegaroons is widely believed and sometimes reported (Eisner et al. 1961; Teruel & Rodríguez-Cabrera 2014). Based on our years of investigation in the field and laboratory, we almost never observed cannibalism and it only occurred during stressful situations. We suspect that the reports of cannibalism involved individuals taken from their natural environment and put together in captivity. To test if cannibalism occurs under field conditions, we constructed enclosures in the natural habitat of vinegaroons. When this was done, cannibalism among adults and last instar immatures was not observed. Cannibalism occurred rarely between adults and third instars under conditions of extreme crowding. To determine if lack of common cannibalism was the result of the risk of injury or death to the attacker, rather than to opportunity, we tested situations where recently-killed individuals were placed with many live individuals in the field arenas. No scavenging of these dead individuals occurred – something that further indicates that cannibalism in nature is rare. Although we did not test with first or second instar individuals in the arenas, we suspect, based on other observations over the years, that the youngest individuals are likely to be at great risk from larger individuals and that risk might be another explanation for the rare observations of first and second instars in the field.

In summary, vinegaroons accept a wide diversity of prey including toxic or venomous prey, as well as other predators within their environment. Only the most well-armored, large, or extremely toxic prey are safe. In turn, adult and fourth instar vinegaroons have few, if any, meaningful predators. Adult vinegaroons are dominant members of the apex predator guild of arthropods in their environment and are not preyed on by any other arthropods. The small first and second instar vinegaroons have low risk of being preyed on, but their long lifecycle and slow development makes them the most vulnerable individuals of the species and explains why they spend little time above ground, where the risks are greatest. Cannibalism among adults and fourth instar individuals does not appear to be an important factor in their natural history, though cannibalism by large individuals might be a factor in the lives of the three youngest instars of vinegaroons.

ACKNOWLEDGMENTS

We thank Bruce D. Taubert for generously allowing us to use his photograph of a vinegaroon spraying a potential assailant and Jillian Cowles, Bill Savary and Bob Jacobson for insightful discussions and manuscript reviews.

LITERATURE CITED

Armas LF, Rivera LG. 2009. Un caso de necrofagia en *Mastigoproctus pelegrini* Armas, 2000 (Arachnida: Thelyphonida). *Boletín Sociedad Entomológica Aragonesa* 45:327–328.

Barrales-Alcalá D, Franke OF. Prendini L. 2018. Systematic revision of the giant vinegaroons of the *Mastigoproctus giganteus* complex (Thelyphonida: Thelyphonidae) of North America. *Bulletin of the American Museum of Natural History* 418:1–62.

Brodie III ED, Brodie Jr. ED. 1999. Predator-prey arms race. *BioScience* 49:557–568.

Carrel JE, Britt EJ. 2009. The whip scorpion, *Mastigoproctus giganteus* (Uropygi: Thelyphonidae), preys on the chemically defended Florida scrub millipede, *Floridobolus penneri* (Spirobolida: Floridobolidae). *Florida Entomologist* 93:500–502.

Creel S, Dröge E, M'soka J, Smit D, Becker M, Christianson D et al. 2017. The relationship between direct predation and antipredator responses: a test with multiple predators and multiple prey. *Ecology* 98:2081–2092.

Cresswell W, Quinn JL. 2013. Contrasting risks from different predators change the overall nonlethal effects of predation risk. *Behavioral Ecology* 24:871–876.

Eisner T, Meinwald J, Monro A, Ghent R. 1961. Defence mechanisms of arthropods – I The composition and function of the spray of the whipscorpion, *Mastigoproctus giganteus* (Lucas) (Arachnida, Pedipalpida). *Journal of Insect Physiology* 6:272–298.

Eklöv P. 2000. Chemical cues from multiple predator-prey interactions induce changes in behavior and growth of anuran larvae. *Oecologia* 123:192–199.

Finke DL, Denno RF. 2002. Intraguild predation diminished in complex-structured vegetation: implications for prey suppression. *Ecology* 83:643–652.

Grabowski JH, Hughes AR, Kimbro DL. 2008. Habitat complexity influences cascading effects of multiple predators. *Ecology* 89:3413–3422.

Harvey MS. 2003. Catalog of the smaller arachnid orders of the world. CSIRO, Collingwood, Australia.

Haupt J, Müller F. 2004. New products of defense secretion in South East Asian whip scorpions (Arachnida: Uropygi: Thelyphonida). *Zeitschrift fur Naturforschaftung* 59:579–581.

Haupt J, Höhne G, Schwarz H, Chen B, Zhao W, Zhang Y. 1988. Chinese whip scorpion using 2-ketones in defense secretion (Arachnida: Uropygi). *Journal of Comparative Physiology B* 157:883–885.

Haupt J, Höhne G, Weiske T. 1993. Acetic acid esters, N-hexanol, N-octanol, and capronic acid as ingredients in the defense secretion product of whip scorpions. *Bollettino delle sedute della Accademia Gioenia di Scienze Naturali in Catania* 26:175–180.

Hoset KS, Koivisto E, Huitu O, Ylönen H, Korpimäki. 2009. Multiple predators induce risk reduction in coexisting vole species. *Oikos* 118:1421–1429.

Itokawa H, Kano R, Kaneko S, Nakajima T, Yasuhara T, Yonabaru S. 1981. Chemical investigation of the spray of the Asian whip scorpion *Typopeltis crucifer* Pocock, 1894. *Japanese Journal of Sanitary Zoology* 32:67–71.

Itokawa H, Kano R, Nakajima T. 1985. Chemical investigation of the spray of the Asian whip scorpion *Typopeltis stimpsoni* (Wood, 1862). *Japanese Journal of Sanitary Zoology* 36:65–66.

Kishida O, Nishimura K. 2005. Multiple inducible defences against multiple predators in the anuran tadpole, *Rana pirica*. *Evolutionary Ecology Research* 7:619–631.

Klecka J, Boukal DS. 2012. Who eats whom in a pool? A comparative study of prey selectivity by predatory aquatic insects. PLoS ONE 7(6):e37741.

Lone K, Mysterud A, Gobakken T, Odden J, Linnell J, Loe LE. 2017. Temporal variation in habitat selection breaks the catch-22 of spatially contrasting predation risk from multiple predators. *Oikos* 126:624–632.

Martin CW, Fodrie FJ, Heck Jr. KL, Mattila J. 2010. Differential habitat use and antipredator response of juvenile roach (*Rutilus rutilus*) to olfactory and visual cues from multiple predators. *Oecologia* 162:893–902.

McIntosh AR, Peckarsky BL. 1999. Criteria determining behaviour responses to multiple predators by a stream mayfly. *Oikos* 85:554–564.

Michalko R, Pekár S, Entling MH. 2019. An updated perspective on spiders as generalist predators in biological control. *Oecologia* 189:21–36

Mukherjee S. Heithaus MR. 2013. Dangerous prey and daring predators: a review. *Biological Reviews* 88:550–563.

Noriega JA, Botero-Trujillo R. 2008. First report of whip scorpions (Arachnida: Uropygi) feeding on dung beetles (Coleoptera: Scarabaeidae). *Boletín Sociedad Entomológica Aragonesa* 42:451–452.

Patten BM. 1917. Reactions of the whip-tail scorpion to light. *Journal of Experimental Zoology* 23:251–275.

Polis GA, Myers CA, Holt RD. 1989. The ecology and evolution of intra guild predation: Potential competitors that eat each other. *Annual Review of Ecology and Systematics* 20:297–330.

Punzo F. 2000. Diel activity patterns and diet of the giant whipscorpion *Mastigoproctus giganteus* (Lucas) (Arachnida, Uropygi) in Big Bend National Park (Chihuahuan Desert). *Bulletin of the British Arachnological Society* 11:385–387.

Punzo F. 2005. Use of a Y-maze to assess the response of the giant whipscorpion *Mastigoproctus giganteus* (Arachnida: Uropygi) to olfactory cues associated with a predator, *Hogna carolinensis* (Araneae: Lycosidae). *Bulletin of the British Arachnological Society* 13:172–174.

Ratcliffe JM, Nydam ML. 2008.Multimodal warning signals for a multiple predator world. *Nature* 445:96–99.

Schmidt JO. 2009. Vinegaroons. Pp. 1038–1041. *In* Encyclopedia of Insects, 2ed. (VH Resh, RT Cardé, eds.). Academic, San Diego, CA.

Schmidt JO, Blum MS. 1977. Adaptations and responses of *Dasymutilla occidentalis* (Hymenoptera: Mutillidae) to predators. *Entomologia Experimentalis et Applicata* 21:99–111.

Schmidt JO, Dani FR, Jones GR, Morgan ED. 2000. Chemistry, ontogeny, and role of pygidial gland secretions to the vinegaroon *Mastigoproctus giganteus* (Arachnida: Uropygi). *Journal of Insect Physiology* 46:443–450.

Schmidt JO, Schmidt LS, Cowles J. 2021. Reproduction and life history of the vinegaroon (*Mastigoproctus tohono*). *J. Arachnology* 49:371–379.

Sherbrooke WC. 2003. Introduction to Horned Lizards of North America. University of California Press, Berkeley, CA.

Teruel R, Rodríguez-Cabrera TM. 2014. Occurrence of cannibalism in *Mastigoproctus pelegrini* Armas, 2000 (Thelyphonida: Thelyphonidae). *Revista Ibérica de Aracnología* 24:115–117.

Thaker M, Vanak AT, Owen CR, Ogden MB, Niemann SM, Slotow R. 2011. Minimizing predation risk in a landscape of multiple predators: effects on the spatial distribution of African ungulates. *Ecology* 92:398–407.

Toledo LF. 2007. Predação e Defesa em Anuros: Revisão, Descrição e Evolução. PhD dissertation, Universidade Estadual Paulista Campus de Rio Claro, Brazil.

Weber DC, Lundgren JG. 2009. Assessing the trophic ecology of the Coccinellidae: Their roles as predators and as prey. *Biological Control* 51:199–214.

Willink B, García-Rodríguez A, Bolaños F, Pröhl H. 2014. The interplay between multiple predators and prey colour divergence. *Biological Journal of the Linnean Society* 113:580–589.

Yogi S, Haupt J. 1977. Analyse des Wehrsekretes bei dem Geisselskorpion *Typopeltis crucifer* Pocock. *Acta Arachnologica* 27:53–56.

Manuscript received 24 January 2021, revised 4 May 2021, accepted 14 May 2021.