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Natural history, phenology, population density, and injuries/regeneration of the vinegaroon (Uropygi: Thelyphonidae: *Mastigoproctus tohono*)

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Abstract. Vinegaroons in the high desert grasslands of southeastern Arizona spend much of the year in deep sealed underground cells and dig to the surface when the first summer rains begin in late June or during July. They are active only at night, when they are large apex ambush predators that prey on a variety of small, surface-dwelling animals. Adult and last instar immature vinegaroons were frequently observed, whereas the smaller first three instars were rarely seen. Using mark-capture techniques, the density of individuals in the area was found to be at least 95 individuals/ha to as high as 680 individual/ha. The population profile remained mostly steady over several years with adults and 4th instar immatures constituting 90% of the observed population. Females were mainly present during the earlier part of the foraging season. In contrast, males were active much longer and until the end of season. The three first instars of vinegaroons spent little time on the surface of the ground partly because they are vulnerable to predators and partly because they require few prey items to accumulate the necessary reserves for molting to the next instar. About 12% of the population had injuries, or signs of previous injuries. Most injuries were to their tail-like flagellum, with a few sensory leg injuries. Short, regrown flagella in field individuals showed their ability to regenerate these lost appendages and laboratory experiments demonstrated that vinegaroons can regenerate lost parts of sensory legs and even their hard, powerful pedipalps.

Keywords: Whipscorpion, *giganteus*, Thelyphonida, whiptail, cannibalism

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Vinegaroons are large arachnid predators found in various tropical and warm regions of the world, including South and East Asia, North and South America, Oceania, and West Africa (Harvey 2003). Much of the literature relates to taxonomic and phylogenetic aspects of the group (e.g., Harvey 2003; Tetlie & Dunlop 2008; Selden et al. 2016; Cai & Huang 2017; Clouse et al. 2017; Barrales-Alcalá et al. 2018; Teruel 2018; Giribet & Edgecombe 2019; Seraphim et al. 2019; Lozano-Fernandez et al. 2020), with some investigations of their morphology (Wolff et al. 2015; Gallant & Hochberg 2017; Freeman & Hochberg 2018; Grams et al. 2018; McLean et al. 2018; Seiter et al. 2018; Lehmann & Melzer 2019), embryology (Yoshikura 1961, 1965), physiology (Ahearn 1970; Crawford & Cloudsley-Thompson 1971; Shultz 1991, 1992), and 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).

Vinegaroon courtship behavior has been studied in detail (Klingel 1963; Weygoldt 1970, 1971, 1972, 1978, 1988; Haupt 1997; Ferreira et al. 2011; Weygoldt & Huber 2013; Watari & Komine 2016; Seiter et al. 2018; Schmidt et al. 2021). In contrast, other vinegaroon behaviors such as prey choice (Toledo 2007; Noriega & Botero-Trujillo 2008; Carrel & Britt 2009; Schmidt & Schmidt 2022) and potential predators (Eisner et al. 1961; Punzo 2005; Schmidt & Schmidt 2022) have received little attention, and the life span and fecundity of vinegaroons has been reported for only two species, the Japanese species *Typopeltis stimpsonii* (Wood, 1862) (Yoshikura 1965) and the North American species *Mastigoproctus tohono* Barrales-Alcalá, Francke and Prendini, 2018 (Schmidt et al. 2021).

The paucity of basic knowledge of vinegaroon behavior and general natural history is partly because vinegaroons are strictly nocturnal creatures that do not fluoresce like scorpions, are not attracted to lights, are dark colored, slow moving, and are rarely seen in their natural habitats. We report here the natural history and basic biology of the vinegaroon *Mastigoproctus tohono* in its natural environment.

[*] Deceased

METHODS

Research area.—A square survey plot 160 m on edge was established in 1996 near Willcox, Cochise County, Arizona, USA 1,279 m above sea level. The area is an overgrazed high desert grassland consisting of mostly flat or gently sloping stabilized and weathered sandy-loam soil. Currently the dominant vegetation consists mainly of burroweed (*Isocoma tenuisecta*), mesquite (*Prosopis velutina*), indigo bush (*Psorothamnus* sp.), and sand sagebrush (*Artemisia filifolia*). In addition to the dominant vegetation, a variety of ephemeral plants and other small perennial plants are present. Exact coordinates of the location are not provided to avoid over-collecting of this population for the pet trade or commercial interests and thereby potentially harming the population and the environment (Marshall et al. 2022).

For the years 1999–2004, soil moisture was measured as the averages of three gypsum block sensors permanently buried in the soil at depths of 10, 30, 50, and 70 cm and recorded with a Delmhorst Model KS-D1 moisture analyzer (Delmhorst Instruments, Towaco, NJ USA). These gypsum block sensors provide only a relative measure of soil moisture which can be easily visualized when the soil is excavated. In this system, "moist" is observed when the soil is a dark gray in color and is assumed to be saturated, whereas "dry" soil is a much lighter gray in color and contains very little water. Almost no gradation of color in this soil is observed between the moist and dry zones.

The temperatures at the research site were measured throughout each visit for the years 1999–2004 at the ground surface level with a Raytek Rayngêr ST8 infrared thermometer (Raytek Corp., Santa Cruz, CA, USA) and at 15 and 30 cm below surface level using 30 cm Comark standard industrial penetration probes (Comark, Hertfordshire, UK). In order to record the maximum and minimum temperatures experienced at the site, particular attention was focused on ensuring visits occurred during both the hottest and coldest days of each year.

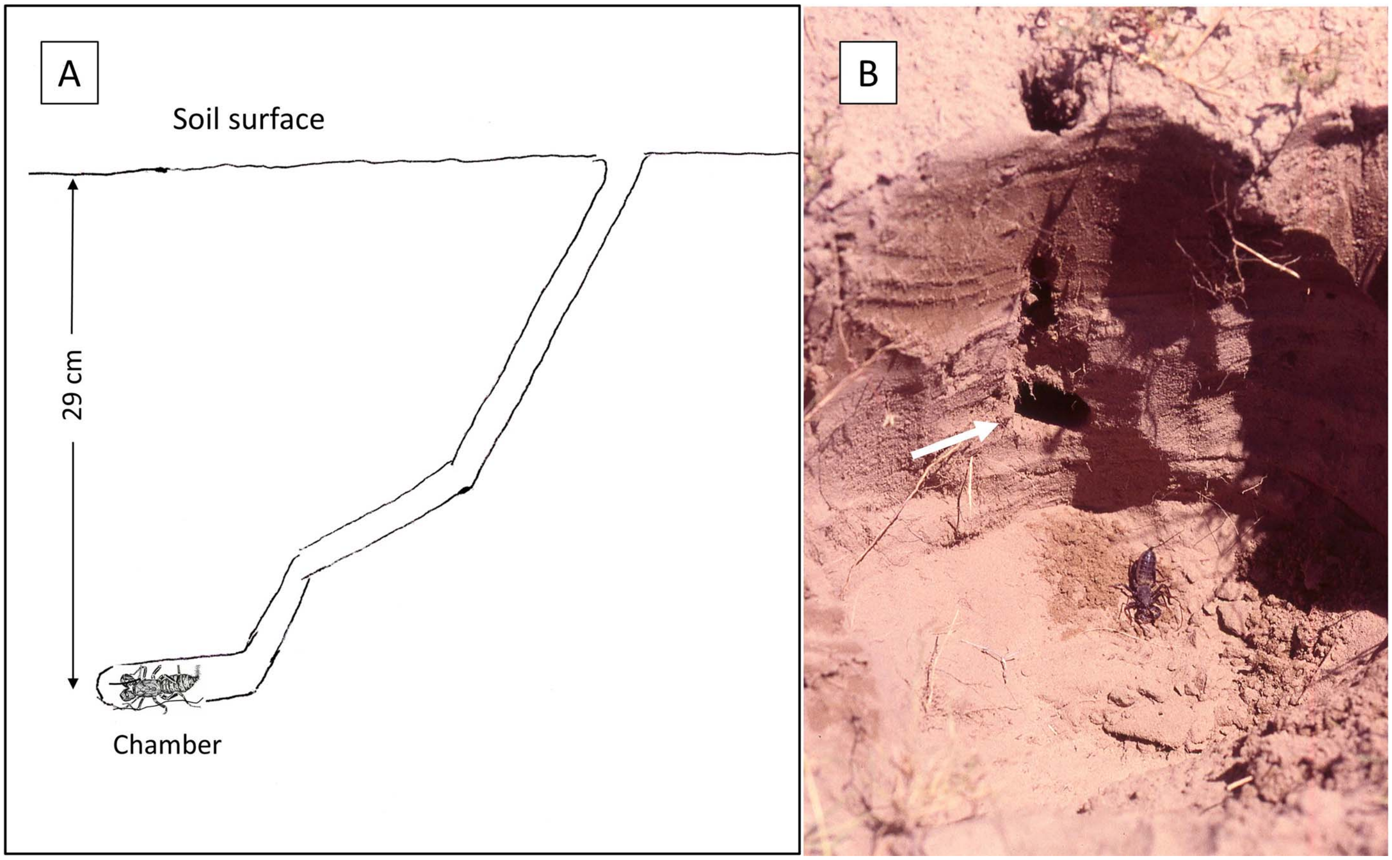

Figure 1.—Vinegaroon underground burrow. (A). Diagram of an adult during the active summer season. (B). Photograph of an excavation of a burrow with the adult below the bottom chamber indicated by the arrow.

Above ground activity and population of vinegaroons.—In 1996, free-ranging individuals of *Mastigoproctus tohono* were captured by hand during nighttime searches in the research area during the summer rainy season that began that year on 1 July and ended about 26 September. Searches continued thereafter until 9 November. Captured individuals were measured for body length (anterior tip of prosoma to the end of the wide segments of the opisthosoma), uniquely marked with colored Liquid Paper (Liquid Paper Corporation, Wilmington DE), and released. The life stage (female, male, 4th instar, 3rd instar 2nd instar or 1st instar) of individuals is easily determined by nonoverlapping lengths of the body and the carapace (Schmidt et al. 2021) and was recorded, as were any injured body parts. Previously marked individuals were recorded as recaptures. Similar surveys were continued in 1997 and 1998 with the change that individuals were not marked. Thereafter, the area was revisited less frequently between the years of 1999 to 2018 and data recorded as above.

Laboratory tests of regeneration of lost body parts.—In 1997 and 1998, adult vinegaroons were collected in the field and maintained in 4 L 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. 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 night, or on the ground during the day in the 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. First and second instar individuals from these adults were reared in smaller jars similar to those used for the adults. Immatures were tested for the ability to regenerate lost parts of sensory legs, walking legs, or pedipalps. For sensory legs, one sensory leg of each of four well-fed 1st instars was severed at the mid-tibia in December 1999 and three days later the other sensory leg was also severed at the mid-tibia. For an injured pedipalp, a 2nd instar individual had its pedipalp severed mid-tibia. For walking legs, each of three 2nd instar individuals had a posterior walking leg severed at the patella. None of these individuals were fed after surgery, and they were then placed in small jars containing deep moist study site soil where they dug overwintering chambers in which they molted to the next instar.

RESULTS

Environmental properties of the research area.—The sandy loam in the research area is soft, nearly uniform, and free of rocks and pebbles, yet is firm enough that it does not collapse upon digging. In this habitat, vinegaroons excavate nests that are approximately 30 cm deep and end in a chamber in which the animal resides during daylight in the active season. At the end of the active season the resident vinegaroon fills the tunnel with soil and resides in the cell at the bottom (Fig. 1).

The temperature in the research area can be hot during the summer, reaching a maximum soil surface temperature of 59.5°C, and during the winter a minimum temperature of −15°C. The soil temperatures at 15 and 30 cm below the surface (where the

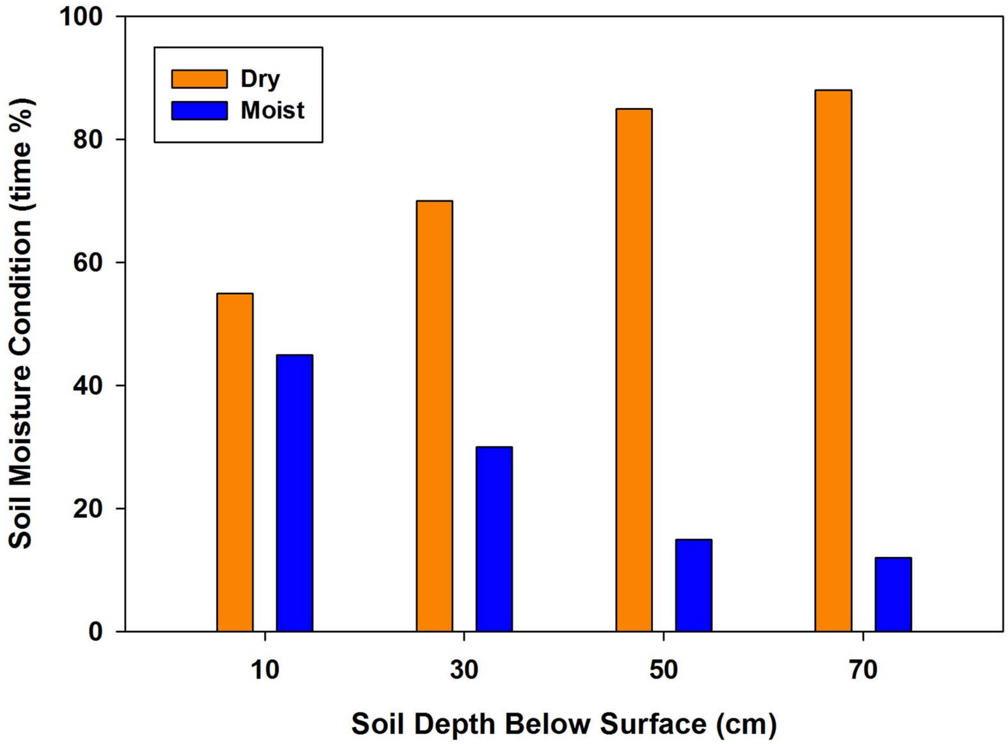

Figure 2.—Soil moisture profile at various depths in the research area based on 52 observations over five years.

vinegaroons are residing) are more moderate and never exceed 38.1°C or below 3.2°C.

The research area is arid, and the soil is often dry. The soil surface stays moist only for a few days after a rain but stays moist longer beneath the surface. The percentages of moist soil in Fig. 2 are estimates derived from periods of time between visits to the research site and serve to represent the general nature of the soil moisture with depth. In general, approximately 45% of the time, the soil is moist at a depth of 10 cm. Often a rain only moistens the upper levels of the soil and fails to penetrate deeply. For example, at 50 cm depth the soil was moist only 15% of the time (Fig. 2).

Above ground activity of vinegaroons.—In 1996, the first vinegaroon was observed above ground on July 1. The last was seen on October 13. During those times we spent 177 hours searching for vinegaroons, and marked and released 244 individuals. The numbers of females, males, and immatures, their median date of appearance on the surface, and the first and last dates recorded on the surface are listed in Table 1. Overall, the largest individuals (females, males, 4th instars) were observed 210 times, whereas the smaller three instars were observed only 34 times. Thus, the larger individuals were spotted over six times as frequently as the small individuals and the youngest and smallest individuals were rarely seen, with only one 1st instar and 11 2nd instars seen. Males tended to remain on the ground surface later in the season than females (23 males versus 5 females after September 7).

Of the 244 marked vinegaroons, 34 were recaptured during the 1996 field season. All of these were large individuals – that is, females, males, and 4th instars. None of the smaller 1st, 2nd, or 3rd instars were recaptured despite 34 of them having been marked. About the same percentage of the populations of females, males, and 4th instars were recaptured (Table 2A). The number of days between being marked and recaptured ranged from 1 day to 60 days with an average of 13 days (see Supplemental Table S1, online at https://doi.org/10.1636/JoA-S-22-044.s1). In general, females were recaptured within a few days of being marked, whereas males and 4th instars were recaptured over longer periods following marking than females (Table 2B). The mean days between captures and recaptures of females was significantly shorter than for males (Mann-Whitney U test, $Z = 2.72$, $P < 0.01$) or 4th instars (Mann-Whitney U test, $Z = 2.97$, $P < 0.05$).

Table 1.—Observations of vinegaroons on the soil surface, 1996.

Life stage	Individuals (n)	Date first observed	Median date observed	Date last observed	Season length (d)
Female	47	1 July	21 July	13 October	105
Male	79	3 July	17 August	7 October	97
4th instar	84	3 July	8 August	13 October	103
3rd instar	22	3 July	6 August	29 September	89
2nd instar	11	3 July	17August	7 September	67
1st instar	1	12 August	12 August	12 August	n/a

Table 2A.—Recaptures of vinegaroons, 1996.

Life stage	Captures (n)	Individuals recaptured (n)	% Recaptured
Female	47	7[a]	14.9
Male	79	14	17.7
4th instar	84	13[b]	15.5
1st, 2nd, 3rd	34	0	0
Total	244	34	13.9

[a] 2 individuals recaptured twice.
[b] 1 recaptured twice, 1 recaptured three times, 1 recaptured four times.

Table 2B.—Time between captures and recaptures of vinegaroons, 1996.

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Life stage	Recaptures (n)	Mean days between captures	S Dev.
Female	7	1.86	0.90
Male	14	15.3	15.9
4th instar	13	17.2	19.3
Total	34	13.2	16.5

We recaptured 13.9 percent of the 244 vinegaroons marked. Based on this recapture rate, the number of vinegaroons in the research area is approximately 1750. This translates into about 680 vinegaroons/ha for the 2.56 ha research area.

The year-to-year variation in the life stage composition of vinegaroons was determined for the years 1996, 1997, 1998, and 1999–2018. The latter period was a combination of sporadic surveys over many years that were combined to yield 161 individuals that could then be compared to the three years of more intensive surveying (Table 3). The percentage composition of females, males, and each of the four immature instars within each time period is shown in Fig. 3. The proportions of the different life stages were similar over the time periods, with two exceptions: (1) females comprised a smaller percentage of the population in 1996 than in the other time periods; and (2) 4th instars constituted a larger percentage of the population in 1996 than in other time periods (Fig. 3). The numbers of individuals of instars 1–3 were too few to allow meaningful conclusions.

Frequency of encountering injured vinegaroons in the field.— Each vinegaroon found in the field was examined for evidence of injury to any body parts. Seventy-three of the 609 individuals encountered (12%) exhibited some type of injury. Females had the highest injury rate at 17.3% of their population, followed by males at 12.6% and 4th instars at 6.8% (Table 4). The percentage composition of injured females, males, and each of the four immature instars for each time period is shown in Fig. 4. The frequencies of injury for the different time periods were similar for females. Compared to other years, males and 4th instars had higher frequencies of injury in 1997. Individuals smaller than 4th instars were too few in number to draw meaningful conclusions concerning their percentages of injury. Most injuries were to the tail (flagellum) (Table 5), a body part that is easily broken or entirely lost when attacked. Eleven percent of the population sustained either partial or total loss of the tail. This figure includes 10 individuals that had shorter tails that had regenerated following previous injuries. Sensory legs were occasionally injured (3.1% in females and 1.9% in males). No immatures sustained injuries to sensory legs. Walking legs were not injured in field-encountered vinegaroons, with the exception of one female that had a missing middle walking leg.

Regeneration of lost body parts.—The ability of vinegaroons to replace a lost tail with a new tail approximately half the normal length was observed in 10 individuals from the field. Other injured body parts were rarely seen, and all of those were in adults, which cannot molt to replace a lost body part. To test the ability of vinegaroons to regrow lost body extremities other than tails, sensory legs, a walking leg and a pedipalp were partially amputated. After molting to 2nd instars, all four of the 1st instars that had both sensory legs amputated at the mid-tibia regrew sensory legs that appeared normal with the exception that they often had one fewer or one extra tarsomere than the normal eight (Table 6). The ability of vinegaroons to regrow replacement walking legs was poorer than their ability to regrow sensory legs, and those that were regrown were either non-functional or poorly functional. One individual not only survived the loss of a third of a pedipalp – it regrew a normal size replacement upon molting with the only noticeable difference being a lighter color of the replaced part.

DISCUSSION

The study site is an ideal habitat for vinegaroons in many ways. The soil is soft and easy to dig burrows in, to avoid the heat of summer and the cold of winter. In the laboratory, 1st instars readily dig in the substrate to a depth of 15 cm, a field depth at which the temperature is not life-threatening and never exceeds 38.1° nor drops below 3°. The habitat provides an abundance of prey, especially during the summer rainy season when there are numerous beetles, moths, caterpillars, crickets, grasshoppers, winged ants and termites, antlion adults, scorpions, spiders, and solifuges, all of which have been shown to be prey of large vinegaroons (Schmidt & Schmidt 2022). It is also a habitat that is nearly free of predators of large vinegaroons, though smaller individuals do have predators in the habitat (Schmidt & Schmidt 2022). Population densities and factors that are important in vinegaroon life cycles are unknown in other habitats, such as along juniper/oak riparian areas, and might be different in important aspects.

Vinegaroons only emerge from their deep underground cells after the first rains of summer. We have visited the study area in the spring and just before the first summer rain at the site for over

Table 3.—Vinegaroon populations observed during various years.

Time period	Female (n)	Male (n)	4th instar (n)	3rd instar (n)	2nd instar (n)	1st instar (n)	Total (n)
1996	47	79	84	22	11	1	244
1997	36	41	25	6	1	4	113
1998	29	32	25	2	3	0	91
1999–2018	50	55	43	12	1	0	161
Total	162	207	177	42	16	5	609
% of total	26.6	34.0	29.1	6.9	2.6	0.8	100

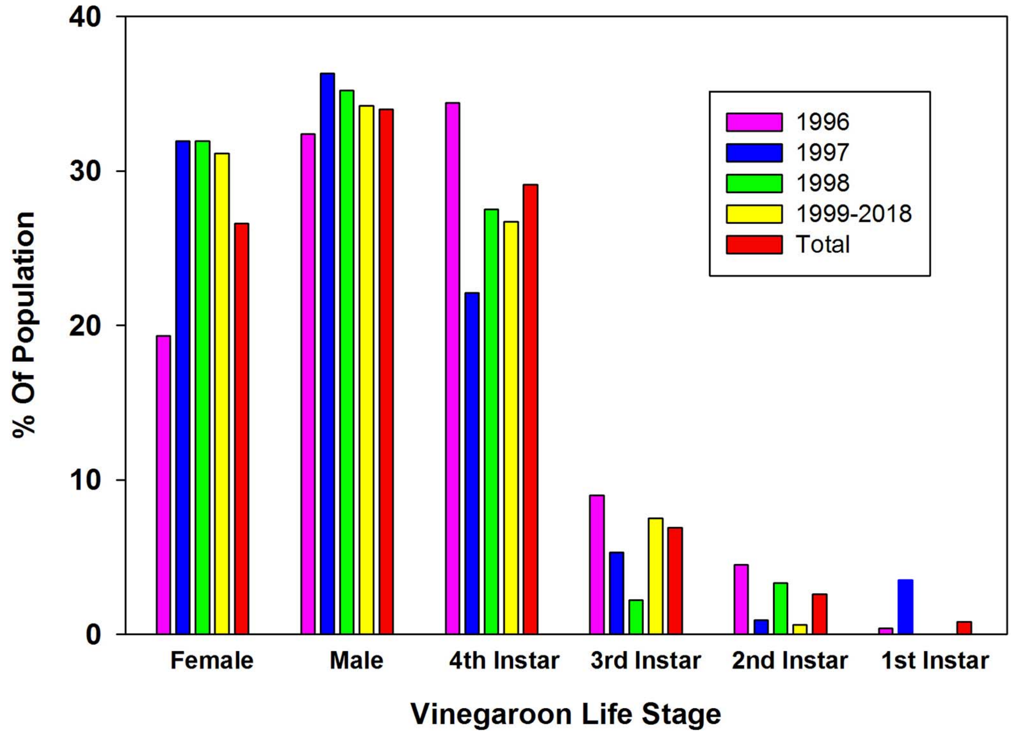

Figure 3.—Composition as a percentage of the population for each of the six vinegaroon life stage types observed above ground during 1996, 1997, 1998, 1999–2018, and for the combined total of all time periods.

20 years and have never seen an individual before the first rain of the season. Once the rains come, the nighttime temperatures are warm, the humidity is high, and all stages of vinegaroons begin appearing above ground. At this time, the area is rich in prey resources as evidenced by the large number of individuals caught and marked in the small area. We actually captured 95 individuals per hectare and that serves as a minimum number in the area. Nothing is known about navigational systems or home ranges of vinegaroons, though the home ranges of most other arachnids are small (Gaffin & Curry 2020; Jones et al. 2022). We suspect that the home ranges of vinegaroons are likewise small compared to the size of the research site and that they are unlikely to move out of the study area (Gaffin & Curry 2020). Therefore, the recapture data support the observation that many individuals were not seen and that based on the recaptures, the calculation of as many as 680 individuals/ha is realistic.

The lifecycle of vinegaroons is at least six years and could be as long as 11 years if immatures cannot find enough prey to gain the body mass necessary for molting to the next stage (Schmidt et al. 2021). This ability to hedge bets by enduring years of low rainfall and prey abundance might be the reason we observed a relatively stable life stage makeup of the population over the years.

The amount of prey in the area appears to be a major factor governing the ultimate vinegaroon population density. The amount of prey likely also explains the presence and length of time that the various life stages are above ground. Females emerge early in the season and tend to disappear relatively quickly compared to males and 4th instars. Females have two requirements they must meet before they return to, and stay, underground – mating and finding enough prey to feed to their new 1st instar offspring (Schmidt et al. 2021) and to accumulate the necessary body reserves for overwintering and producing a cluster of eggs. Once they have achieved these goals, staying above ground would increase the risk of injury or death. Males, on the other hand, require only enough captured prey to sustain themselves, but need to spend as much time searching for potential mates as possible – hence, the presence mainly of males in the later times of the season when they still have a small chance of finding a female with which to mate. Fourth instars are relatively safe from predators but need to find enough prey to gain the body mass necessary for molting to an adult. Once they have achieved this, they, like the females,

Table 4.—Injuries of vinegaroons observed in the field during various years.

Year(s)	Female (n)	Male (n)	4th instar (n)	3rd instar (n)	2nd instar (n)	1st instar (n)	Total (n)
1996	9	9	4	1	2	0	25
1997	7	8	4	1	0	0	20
1998	4	3	1	0	1	0	9
1999–2018	8	6	3	2	0	0	19
Total	28	26	12	4	3	0	73
Population	162	207	177	42	16	5	609
% Populat.	17.3	12.6	6.8	9.5	18.8	0	12.0

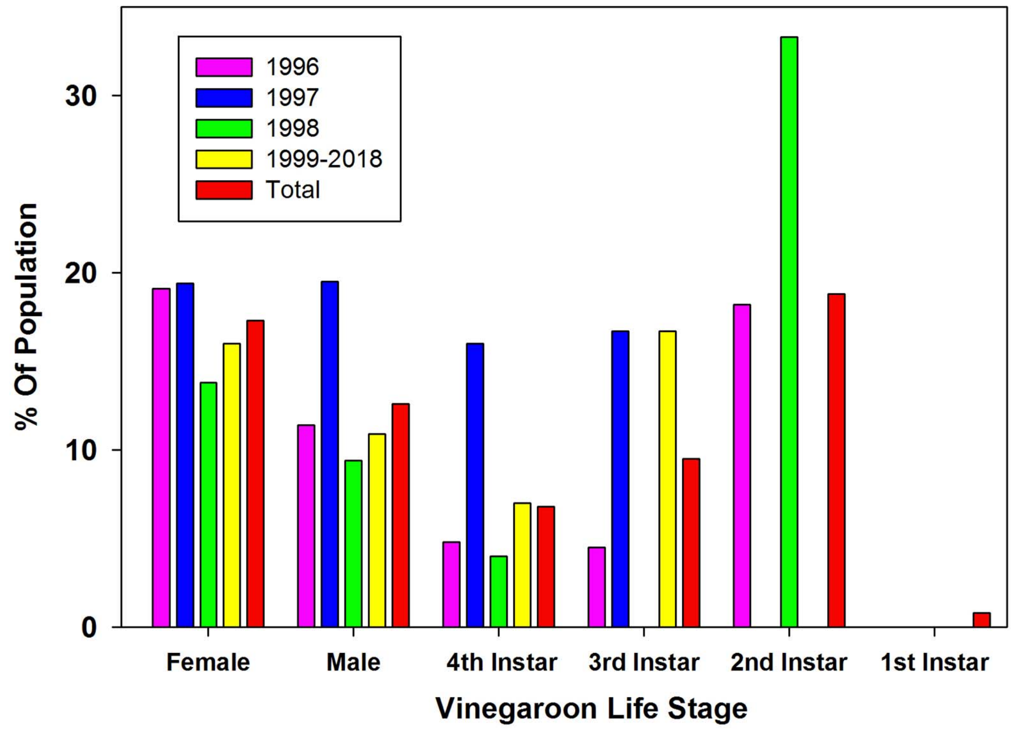

Figure 4.—Composition as a percentage of injured individuals of vinegaroons for each of the six vinegaroon life stage types observed above ground during 1996, 1997, 1998, 1999–2018, and for the combined total of all time periods.

should avoid remaining above ground. The three smallest instars of vinegaroons present an interesting situation. We rarely saw 1st, 2nd, or 3rd instars above ground, something that has been noted by other naturalists (Punzo 2000; personal discussions). Two factors appear related to these observations. First, unlike large individuals of the species, small ones are susceptible to predation by large spiders and other arthropods, amphibians, and cannibalism by larger vinegaroons (Schmidt & Schmidt 2022). The small vinegaroons would benefit by spending as little time subjected to these risks as possible. Second, since vinegaroons from this habitat do not ever molt twice in a year and much of the prey in the environment is their size or smaller (Schmidt & Schmidt, unpublished), they can quickly gain enough resources from only a few prey items to enable them to molt to the next instar the following spring.

Many vinegaroons in the research site showed evidence of having survived after bodily injuries. Evidence included the partial or total loss of their tails, the presence of regrown tails from loss during a previous season, and missing parts of their sensory legs. Vinegaroon tails are sensory organs that enable them to detect predatory threats from behind. They might also help orient the direction in which their defensive vinegary spray is aimed, although the tail is not necessary for directing their defensive spray. Individuals that have autotomized their tails are capable of spraying in appropriate directions (Eisner et al. 1961; personal observations). Sensory legs are used to actively explore the environment around the individual and, thus, are susceptible to being attacked and injured by potential predators. Female sensory legs are also held in the pedipalps of males during courtship and could be injured at that time (Haupt 1997). Male sensory legs are used much less in courtship and would be expected to receive few injuries. We did, however, observe one situation in which a female severed a male sensory leg during a failed courtship (personal observation). We cannot know how frequently sensory legs are lost due to attacks by predators versus being injured during courtship, though our experience suggests that injury during courtship is extremely rare (Schmidt et al. 2021). Only one individual in the field environment was seen missing a walking leg. Whether that leg loss was from an attack by a predator or was from a molting or congenital problem is unknown. The rarity of walking leg losses indicates that predator attacks to the sides of vinegaroons are uncommon, or that those that do occur might be lethal to the vinegaroon and thus not leave evidence.

Spiders are well-known for their ability to regrow lost legs or pedipalps after molting (Fleming et al. 2007; Fraser et al. 2020). The

Table 5.—Injured body parts of vinegaroons observed in the field from 1996–2018.

Body part injured	Female (n)	Male (n)	4th instar (n)	3rd instar (n)	2nd instar (n)	1st instar (n)	Total (n)
Tail (flagellum)	25	23	12	4	3	0	67
Sensory leg	5	4	0	0	0	0	9
Walking legs	1	0	0	0	0	0	1
Population (n)	162	207	177	42	16	5	609
% Injured tail	15.4	11.1	6.8	9.5	18.8	0	11.0
% Injured sensory legs	3.1	1.9	0	0	0	0	1.48
% Injured walking legs	0.62	0	0	0	0	0	0.16

Table 6.—Regeneration of vinegaroon extremities in the laboratory.

Anatomy removed (instar tested)	Wt (mg) before regeneration	Wt (mg) of new instar	Results and comments
Sensory legs at mid-tibia			
#1 (1st instar)	275.4	255.8	Completely regrown, but with 8 & 9 tarsomeres; matured to male, lived 3 years as adult
#2 (1st instar)	213.7	256 .6	Completely regrown, with 8 & 8 tarsomeres; died 3rd instar
#3 (1st instar)	190.0	214.3	Completely regrown, but with 7 & 8 tarsomeres; died a month later
#4 (1st instar)	285.3	254.3	Completely regrown, but with 8 & 9 tarsomeres; matured to male, lived 4 years as adult
Pedipalp at mid-tibia			
#1 (2nd instar)	357.7	455.6	Pedipalp regrown, but regrown part more reddish than other; died a month later
Posterior walking leg at patella			
#1 (2nd instar)	419.1	535.2	Regrown leg shorter, functioned poorly; died 3 months later
#2 (2nd instar)	385.3	478.1	Regrown leg only as a non-functional stump; died 1 month later
#3 (2nd instar)	537.9	618.2	Regrown leg shorter, functioned poorly; died later that year

regeneration of lost body parts in vinegaroons has been little explored. Our surgical removal of about half of both sensory legs demonstrated that individuals lacking much of their sensory legs could still orient and successfully dig overwintering chambers, molt, and regrow normal-appearing sensory legs. The regrowth was not perfect in that many of these individuals had fewer or more tarsomeres at the tip of their sensory legs than normal. Our few individuals that had parts of walking legs removed did not regenerate good functional replacement legs. This finding of an inability to replace a functional walking leg deserves re-examination. The pedipalps of vinegaroons are armored, hard appendages used for prey capture and holding. They would not be expected to be severed or lost and, if they were, the animal would not be expected to survive. Nevertheless, based on our one individual that had a pedipalp partially removed, it did regenerate a normal functional replacement which indicates that vinegaroons are capable of regrowing portions of lost pedipalps.

Spadefoot and other toads are abundant and active at night in the study area. They might be major predators of 1st instar vinegaroons simply because of their large numbers. Large wolf spiders and theraphosid spiders also inhabit the area as do scorpions, solifuges and other large arthropods and these predators all present a risk to the smallest vinegaroons. This might explain the observations that 1st and 2nd instar vinegaroons are almost never seen in the field (Punzo 2000; Schmidt & Schmidt unpublished data) and 3rd instars are rarely observed. Although the occurrence of cannibalism among vinegaroons has been widely believed among biologists and sometimes reported (Eisner et al. 1961; Teruel & Rodríguez-Cabrera 2014), our research in the field and laboratory revealed that the killing and/or cannibalism among adult and 4th instars is exceedingly rare (Schmidt & Schmidt 2022). However, cannibalism of the first three immature instars by large individuals does occur (personal observations) and might be part of the reason why the three youngest instars of vinegaroons limit their exposure time above ground.

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SUPPLEMENTAL MATERIALS

Supplemental Table S1, Natural history, phenology, population density, and injuries/regeneration of the vinegaroon (Uropygi: Thelyphonidae: *Mastigoproctus tohono*); online at https://doi.org/10.1636/JoA-S-22-044.s1

LITERATURE CITED

Ahearn GA. 1970. Water balance in the whipscorpion, *Mastigoproctus giganteus* (Lucas) (Arachnida, Uropygi). *Comparative Biochemistry and Physiology* 35:339–353.

Barrales-Alcalá D, Francke 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.

Cai C, Huang D. 2017. A new genus of whip-scorpions in Upper Cretaceous Burmese amber: Earliest fossil record of the extant subfamily Thelyphoninae (Arachnida: Thelyphonida: Thelyphonidae). *Cretaceous Research* 69:100–105.

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.

Clouse RM, Branstetter MG, Buenavente P, Crowley LM, Czekanski--Moir J, Emmanuel D, et al. 2017. First global molecular phylogeny biogeographical analysis of two arachnid orders (Schizomida and Uropygi) supports a tropical Pangean origin and mid-Cretaceous diversification. *Journal of Biogeography* 44:2660–2672.

Crawford CS, Cloudsley-Thompson JL. 1971. Water relations and desiccation-avoiding behavior of the vinegaroon *Mastigoproctus giganteus* (Arachnida: Uropygi). *Entomologia Experimentalis et Applicata* 14:99–106.

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.

Ferreira RL, de Castro Silva W, Vieira VC, Silva EMS. 2011. Aspects of the behavior and reproduction of *Mastigoproctus brasilianus* Koch, 1843, (Arachnida: Uropygi: Thelyphonidae). *Revista de Etologia* 10:3–11.

Fleming PA, Muller D, Bateman PW. 2007. Leave it all behind: a taxonomic perspective of autotomy in invertebrates. *Biological Reviews* 82:481–510.

Fraser C, Wede J, Uetz GW. 2020. Limb autotomy and regeneration affect vibratory/seismic courtship signaling and female receptivity in wolf spiders. *Journal of Arachnology* 48:132–139.

Freeman J, Hochberg R. 2018. Structure and functional morphology of the acid-secreting pygidial glands in the whipscorpion *Mastigoproctus giganteus* (Lucas, 1835) (Arachnida: Thelyphonida). *Zoomorphology* 137:85–103.

Gaffin DD, Curry CM. 2020. Arachnid navigation – a review of classic and emerging models. *Journal of Arachnology* 48:1–25.

Gallant J, Hochberg R. 2017. Elemental characterization of the exoskeleton in the whipscorpions *Mastigoproctus giganteus* and *Typopeltis dalyi* (Arachnida: Thelyphonida). I*nvertebrate Biology* 136:345–359.

Giribet G, Edgecombe GD. 2019. The phylogeny and evolutionary history of arthropods. *Current Biology* 29:592–606.

Grams M, Wirkner CS, Runge J. 2018. Serial and special: Comparison of podomeres and muscles in tactile vs walking legs of whip scorpions (Arachnida, Uropygi). *Zoologischer Anzeiger* 273:75–101.

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

Haupt J. 1997. A self-made taxonomic character in whip scorpions (Arachnida, Uropygi: Thelyphonida). *Proceedings of the 16th European Colloquium of Arachnology*:107–111.

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.

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.

Jones RR, Batista-Perales DL, Garcia, EL. 2022. Home on the range: a pilot study on solifuge (Solifugae: Eremobatidae) site fidelity at Rocky Mountain Arsenal National Wildlife Refuge. *Journal of Arachnology* 50:47–50.

Klingel H. 1963. Mating and maternal behavior in *Thelyphonus caudatus* L. (Pedipalpi, Holopeltidia, Uropygi). *Treubia* 26:65–69.

Lehmann T, Melzer RR. 2019. The visual system of Thelyphonida (whip scorpions): Support for Arachnopulmonata. *Arthropod Structure and Development* 51:23–31.

Lozano-Fernandez J, Tanner AR, Puttick MN, Vinther J, Edgecombe GD, Pisani D. 2020. A Cambrian-Ordovocian terrestrialization of arachnids. *Frontiers in Genetics* 11(182):1–11.

Marshall BM, Strine CT, Fukushima CS, Cardoso P, Orr MC, Hughes AC. 2022. Searching the web builds fuller picture of arachnid trade *Communications Biology* (2022) 5:448. https://doi.org/10.1038/s42003-022-03374-0

McLean CJ, Garwood RJ, Brassey CA. 2018. Sexual dimorphism in the Arachnid orders. *PeerJ* 6:e5751. https://doi.org/10.7717/peerj.5751

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.

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.

Schmidt JO, Schmidt LS. 2022. Vinegaroons (Uropygi: *Mastigoproctus tohono*) in a multi-predator/multi-prey system: Prey, predators, and cannibalism *J. Arachnology*. 50:267–276.

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.

Seiter M, Löscher A, Handschuh S, Schwaha T. 2018. First description of spermatophore morphology and mating behavior in *Mastigoproctus proscorpio* (Uropygi) (Latreille, 1806) from Hispaniola, Greater Antilles. *Zoologischer Anzeiger* 273:65–74.

Selden PA, Dunlop JA, Simonetto L. 2016. A fossil whip-scorpion (Arachnida: Thelyphonida) from the upper Carboniferous of the Carnic Alps (Friuli, NE Italy). *Research in Paleontology and Stratigraphy* 122:7–12.

Seraphim G, Ponce de Leao Giupponi A, Silva de Miranda G. 2019. Taxonomy of the thelyphonid genus *Typopeltis* Pocock, 1894, including homology proposals for the male gonopod structures (Arachnida, Thelyphonida, Typopeltinae). *ZooKeys* 848:21–39.

Shultz J. 1991. Evolution of locomotion in Arachnida: The hydraulic pressure pump of the giant whipscorpion, *Mastigoproctus giganteus* (Uropygi). *Journal of Morphology* 210:13–31.

Shultz J. 1992. Step-coupled fluctuations in prosomal pressure may constrain stepping rates in whipscorpions (Uropygi). *Journal of Arachnology* 20:148–150.

Teruel R. 2018. The true generic identity of *Mastigoproctus pelegrini* Armas, 2000: a new genus of Antillean whipscorpions (Thelyphonida: Thelyphonidae). *Ecologica Montenegrina* 17:1–13.

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

Tetlie OE, Dunlop JA. 2008. *Geralinura carbonaria* (Arachnida: Uropygi) from Mazon Creek, Illinois, USA, and the origin of subchelate pedipalps in whip scorpions. *Journal of Paleontology* 82:299–312.

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

Watari Y, Komine H. 2016. Field observation of male-male fighting during a sexual interaction in the whip scorpion *Typopeltis stimpsonii* (Wood 1862) (Arachnida: Uropygi). *Acta Arachnologica* 65:49–54.

Weygoldt P. 1970. Courtship behaviour and sperm transfer in the giant whip scorpion, *Mastigoproctus giganteus* (Lucas) (Uropygi, Thelyphonidae). *Behaviour* 36:1–8.

Weygoldt P. 1971. Notes on the life history and reproductive biology of the giant whip scorpion, *Mastigoproctus giganteus* (Uropygi, Thelyphonidae) from Florida. *Journal of Zoology, London* 164:137–147.

Weygoldt P. 1972. Spermatophorenbau und Samenübertragung bei Uropygen (*Mastigoproctus brasilianus* C. L. Koch) und Amblypygen (*Charinus brasilianus* Weygoldt und *Admetus pumilio* C. L. Koch) (Chelicerata, Arachnida). *Zeitschrift für Morphologie und Ökologie der Tiere* 71:23–51.

Weygoldt P. 1978. Paarungsverhalten und Spermatophorenmorphologie bei Geiβelskorpionen: *Thelyphonellus amazonicus* Butler und *Typopeltis crucifer* Pocock (Arachnida, Uropygi). *Zoomorphologie* 89:145–156.

Weygoldt P. 1988. Sperm transfer and spermatophore morphology in the whip scorpion *Thelyphonus linganus* (Arachnida: Uropygi: Thelyphonidae). *Journal of Zoology, London* 215:189–196.

Weygoldt P, Huber S. 2013. Sperm transfer and maternal care in *Thelyphonus* c. f. *caudatus* from Lombok, Indonesia (Arachnida, Uropygi, Thelyphonida). *Zoologischer Anzeiger* 252:348–349.

Wolff JO, Huber SJ, Gorb SN. 2015. How to stay on mummy's back: Morphological and functional changes of the pretarsus in arachnid postembryonic stages. *Arthropod Structure and Development* 44:301–312.

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

Yoshikura M. 1961. The development of a whip scorpion, *Typopeltis stimpsonii* Wood. *Acta Arachnologica* 17:19–24.

Yoshikura M. 1965. Postembryonic development of a whip-scorpion, *Typopeltis stimpsonii* (Wood). *Kumamoto Journal of Science, Series B, Section 2* 7(2):21–51.

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