ARMS RACES BETWEEN BARK SCORPIONS AND GRASSHOPPER MICE: THE SANTA RITAS AS A "HOT SPOT"

Ashlee H. Rowe[1] & Matthew P. Rowe[2]

[1]*Univ. Texas-Austin*, [2]*Sam Houston State Univ.*

Fig. 1. A representative bark scorpion, *Centruroides exilicauda*. Photo by R.W. Van Devender.

Fig. 2. Southern grasshopper mouse, *Onychomys torridus*, consuming a bark scorpion.

Background

Bark scorpions (*Centruroides* spp., Fig. 1) are a dominant component of lithic North American deserts; indeed, in many regions their biomass exceeds that of all vertebrates combined, and may be second only to termites. In short, they represent a large standing crop for predators capable of overcoming the scorpions' defenses. Although bark scorpion venoms are a cocktail of various salts and peptides, they are best known for possessing potent neurotoxins that are specific, and often times lethal, to vertebrates. Why bark scorpions produce vertebrate-specific neurotoxins has been an unresolved mystery, in part because they feed almost exclusively on invertebrates.

The geographical distribution of grasshopper mice (*Onychomys* spp., Fig. 2) overlaps extensively with bark scorpions (Fig. 3). Given that grasshopper mice are voracious predators of arthropods, and historically were known as scorpion mice, a reasonable hypothesis is that these mice may be one of the targets of the bark scorpions' neurotoxins. But do grasshopper mice actually attack and consume such potentially lethal prey? If so, do they get stung, or do they deftly avoid envenomation by first disabling a scorpion's tail? We conducted feeding trials (outlined below) to answer this question.

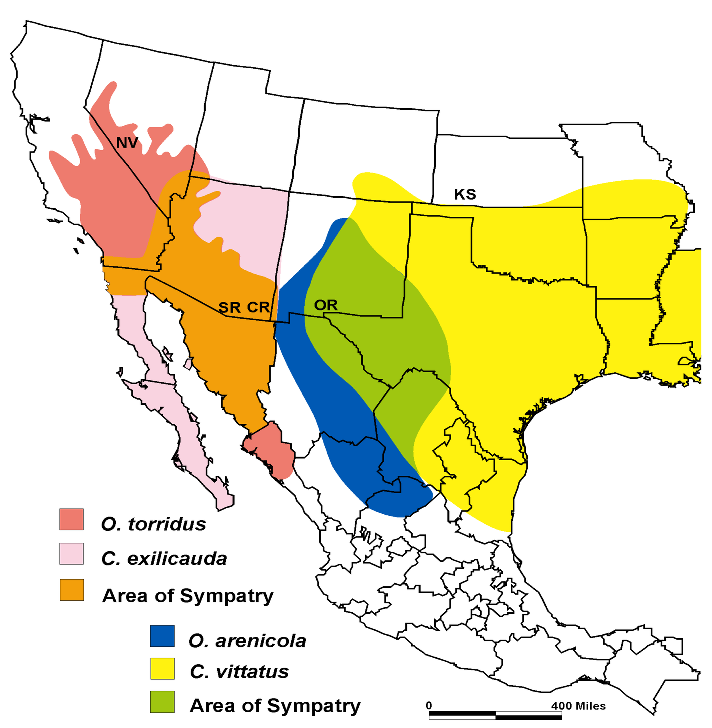

Fig. 3. Distribution of bark scorpions and grasshopper mice, showing broad regions of sympatry between *C. exilicauda* with *O. torridus* and *C. vittatus* with *O. arenicola*. Abbreviations represent our various study sites. SR = the Santa Rita Experimental Range.

Feeding Trials

We conducted feeding trials in the field using wild-caught grasshopper mice from two locations (SR and OR; Fig. 3). Each mouse was tested with three prey items representing differing levels of dangerousness: (1) a harmless field cricket (*Gryllus* or *Acheta* spp); (2) a local stripe-tailed scorpion (*Vaejovis* spp.) which are painful but lack neurotoxins; and (3) a local bark scorpion. In short, we found that grasshopper mice attacked, killed, and consumed bark scorpions as voraciously as crickets or vaejovids, but had a much harder time handling the bark scorpions (Fig. 4). Moreover, the mice were frequently stung.

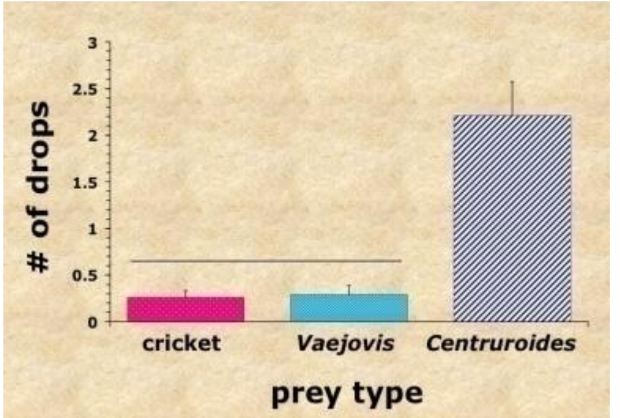

Fig. 4. Number of times grasshopper mice dropped prey items during staged feeding trials. ($F = 39.9$; $df = 1.6, 49.9$; $P < 0.0005$); from Rowe & Rowe 2006. The painful sting of bark scorpions frequently caused the mice to drop the scorpion, significantly increasing the handling time for *Centruroides*.

Venom Resistance

Feeding trials showed that grasshopper mice are resistant to natural stings by bark scorpions. We conducted toxicity tests on five populations of grasshopper mice to confirm their resistance. While all five populations demonstrated resistance to bark scorpion venom compared to non-resistant *Mus musculus*, intra- and interspecific differences exist among populations in their degree of resistance (Fig. 5). These geographic patterns of resistance covary with the presence of *C. exilicauda* and *C. vittatus*. Within the geographic mosaic of the predator-prey system, the Santa Ritas appear to be a "hotspot" characterized by the most neurotoxic population of scorpion and the most resistant population of grasshopper mice we have studied.

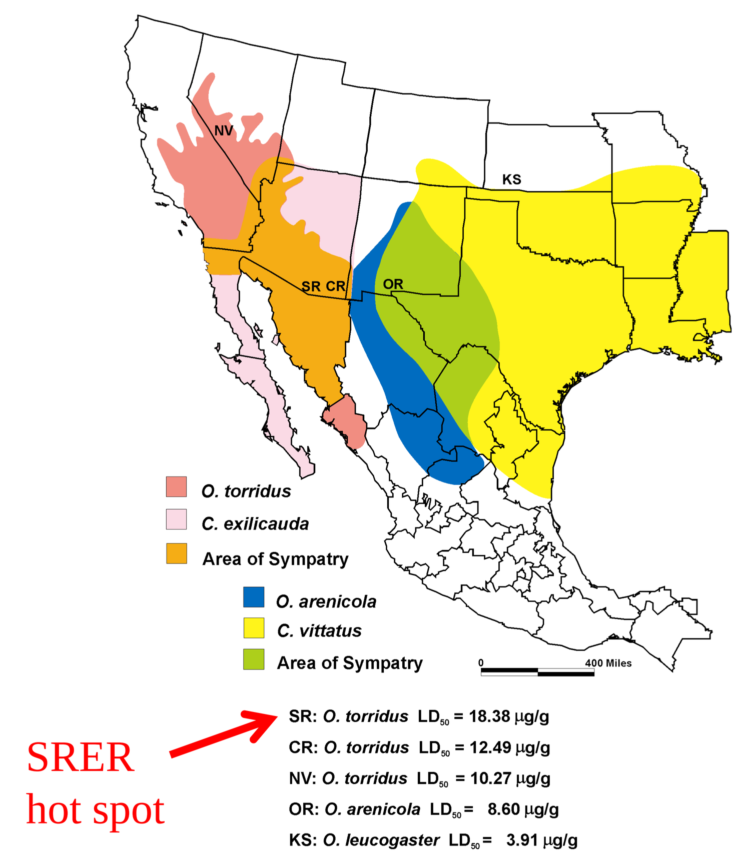

Fig. 5. Physiological resistance of grasshopper mice to *C. exilicauda* venom. Values are shown as the dose of venom that produces mortality in 50% of the mouse population (LD_{50}). By comparison, the LD_{50} for a group of non-resistant *Mus musculus* (strain = CD-1) is ~ 1 µg/g. From Rowe & Rowe 2008.

Venom Painfulness

Geographical patterns of venom resistance in the mice and venom toxicity in the scorpions are consistent with an arms race. Indeed, high levels of resistance in the mice suggests they may have won this battle. Is there any evidence that bark scorpions have responded evolutionarily to venom resistance in their predators? In short, yes – selection may have favored scorpions with significantly more painful stings.

We used a bioassay (foot-licking) to quantify the level of pain induced by venom from bark scorpions and from non-toxic scorpions. We injected small amounts (17µg of venom protein in 10µl of distilled water) of *Centruroides* venom, *Vaejovis* venom, or distilled water into the hind paw of *Mus musculus* and measured the duration of foot-licking during a 10-min post injection period (Fig. 6). Not surprisingly, scorpion venom caused more irritation than did the water. Additionally, *Centruroides* venom engendered more foot-licking by the mice than did venom from *Vaejovis*, a scorpion genus lacking neurotoxic venom. Most intriguing, however, was the more intense irritation caused by the venom from *C. vittatus* relative to *C. exilicauda*, as the latter's venom is significantly more neurotoxic.

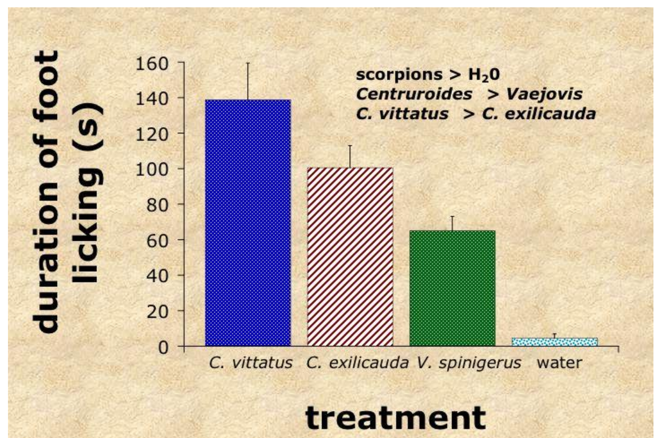

Fig. 6. Total duration of foot-licking by *Mus musculus* (strain CD-1, n = 8 mice per treatment) injected with equivalent volumes and concentrations of venom from two species of bark scorpions (*Centruroides vittatus & C. exilicauda*), a stripe-tailed scorpion (*Vaejovis spinigerus*), and distilled water ($F = 20.0$; $df = 3, 28$; $P < 0.0001$; significant planned contrasts shown above histogram).

Field Evidence

Is there any evidence that painful venom protects scorpions from grasshopper mouse predation in the field? We collected fecal pellets from 30 wild-caught grasshopper mice from two abutting habitats in the SRER: the first a rocky bajada (Fig. 7) teeming with *Centruroides* (73.2 bark scorpions/search hour); the second a mesquite flat (Fig. 8) lacking bark scorpions but sparsely populated with other non-toxic scorpion genera (e.g., *Vaejovis*, 12.7 scorpions/search hour).

Fig. 7. Rocky bajada densely populated with bark scorpions. Fecal pellets collected from 11 grasshopper mice.

Fig. 8. Mesquite flat devoid of bark scorpions. Fecal pellets collected from 19 grasshopper mice.

The proportion of mice whose pellets contained scorpion exoskeleton (assessed using UV light; Fig. 9) was significantly different in the two habitats ($z = 2.38$; $P < 0.02$); 59.1% from the mesquite flats had scorpion remains compared to only 9.1% from the rocky bajada.

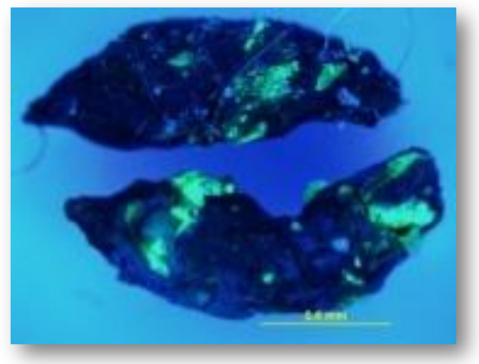

Fig. 9. Grasshopper mouse fecal pellets showing fluorescent scorpion exoskeleton under UV light.

Conclusions

- Grasshopper mice attack and consume toxic bark scorpions as readily as non-toxic prey.
- Physiologically resistance to venom enables mice to exploit this abundant food resource.
- Geographical patterns of venom resistance in the mice and venom toxicity in the scorpions are consistent with an arms race.
- In response to predation, selection may have favored bark scorpions with intensely painful stings that get them dropped.

Current Work

Is there any evidence that grasshopper mice have evolved resistance to pain components in bark scorpion venom? To answer that question, we are currently isolating and identifying pain-inducing toxins from bark scorpion venom and testing grasshopper mice for resistance to those pain-inducing toxins. Our current work is also focused on determining the molecular genetic basis of resistance in grasshopper mice to bark scorpion neurotoxins. We are cloning and sequencing genes from grasshopper mice that encode Na^+ and K^+ ion channels expressed in nerve and muscle (i.e., the targets of the neurotoxins).