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Big, bad, and red: Giant velvet mite defenses and life strategies (Trombidiformes: Trombidiidae: *Dinothrombium*)

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Abstract. Giant velvet mites, the largest living mites, are a familiar sight when they are present above ground, usually after the first summer rains, in warm arid areas. Despite their often-conspicuous presence in enormous numbers, little is known about their basic biology, life history strategies, or predators. The emergence of *Dinothrombium magnificum* (LeConte, 1852) in southern Arizona, USA usually occurs after the first summer rain that exceeds 1 cm. Of the 17 species of vertebrate predators offered velvet mites, only those that quickly engulf their prey intact (horned lizards and toads) successfully preyed upon the mites. Even those ate only one or few before rejecting subsequent mites. Of the 12 species of insect predators and 11 species of other arthropod predators offered mites, only the larvae of antlions were possibly meaningful predators. Nevertheless, antlion larvae only rarely succeeded in puncturing the rubbery integument of a mite and killing it. When sampled by an author, a velvet mite produced an exceedingly bitter, astringent, and spicy taste that endured in the mouth for about an hour. Overall, velvet mites appear to have no meaningful predators, likely because of their enormous suite of highly effective defensives: red aposematic coloration, aposematic odor, a tough puncture-resistant integument, unpleasant tasting chemicals on the integument, and exceedingly distasteful internal compounds.

Keywords: Aposematic, *Dinothrombium magnificum*, distasteful, predation, cannibalism

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Giant velvet mites (Fig. 1), *Dinothrombium* spp., are the world's largest mites before feeding (Makarieva et al. 2005; Dunlop et al. 2018). Engorged ticks after a full blood meal can be larger—up to 2 cm in length (Proctor & Walter 2018)—than giant velvet mites but in the pre-feeding state ticks are much smaller. The largest individuals in the genus are those of *Dinothrombium tinctorium* (Linnaeus, 1767) that can reach a length of 1.4 cm (Cloudsley-Thompson 1962; Dunlop et al. 2018). These spectacular mites can also be present in enormous numbers including one report of a red area on the ground spotted from the air at 500 m that turned out to be an estimated 3–5 million giant velvet mites within an area of 0.8 hectares (Newell & Tevis 1960). Nevertheless, little is known about their biology and adaptations for survival. This is despite the fact that they are large, red, aposematic, highly conspicuous on the surface of the ground, have an extremely noisome taste and repellent smell (C. Starr, pers. comm.; this report), and have few, if any, predators in the adult stage (Schmidt 2009). Even the taxonomy and phylogeny of this small genus is confusing, with some authors listing as many as 17 species (Mąkol 2000) to as few as six species (Mąkol 2007; Mąkol & Wohltmann 2012) and the genus likely contains many more undescribed species (Welbourn 1985, 2021 personal communication; Zhang 1995, 1998).

The genus *Dinothrombium* Oudemans, 1910, is geographically widespread with presence on all continents except Antarctica. The mites are found mainly in sandy deserts. But despite their living in highly arid and often hot environments, they lose water readily (Cloudsley-Thompson 1962) and have continuous gas exchange when they are active which increases water loss (Lighton & Duncan 1995). The mites have also attracted the interest of biochemists who took advantage of the large size of individuals to study the lipoproteins in their blood (Haunerland & Bowers 1989) and pharmacologists and practitioners of traditional medicine who used and investigated extracts of *D. tinctorium* for medical problems such as liver and kidney failure (Salim et al. 2020).

Knowledge of the biology of giant velvet mites is limited because they are only sporadically and briefly present above ground and lack economic importance. The best-studied species usually emerge from their underground burrows after the first heavy rains of summer (or winter in areas with sparse summer rains) and are active on the surface for only several hours in the morning to near midday for one to three days after a rain that brings contemporaneous flights of reproductive termites (Newell & Tevis 1960; Cloudsley-Thompson 1962; Tevis & Newell 1962). The adults are reported to feed only on reproductive termites (Newell & Tevis 1960; Polis et al. 1986) and that is believed to be the reason for the simultaneous flights of termites and emergence of mites. The mites presumably also find mates during this time, though details are unknown (Tevis & Newell 1962; Newell 1979). Eggs of *D. pandorae* (Newell & Tevis, 1960) are laid at the bottom of their burrows in April and hatch into 180–200 µm long larvae 4–6 weeks later. Adults are believed to live at least another two or three years after laying eggs and continue to molt (Newell & Tevis 1960; authors' personal observations). The number of eggs laid ranges from several thousand for *D. pandorae* to a maximum of 100,000 for *D. tinctorium* (Zhang 1998). The larvae of *D. pandorae* attach to and feed on a variety of grasshoppers (Tevis & Newell 1962). The larvae of some species are parasitic on spiders, solifugids, beetles, and Lepidoptera (Fain 1991; Zhang 1998; Vazques-Rojas et al. 2015), and might include other taxa (Felska et al. 2018).

We describe here predator-prey relationships of giant velvet mites, their defensive adaptations against predation, and document the natural history of a species that is active after the first summer rains.

Figure 1.—Giant velvet mite, likely *Dinothrombium magnificum*. Photograph courtesy of Jillian Cowles.

METHODS

Animals.—Adult velvet mites, likely *Dinothrombium magnificum* (LeConte, 1852) (C. Welbourn, pers. comm.), were observed and captured on the soil surface in the morning hours after a previous day's rain in the Willcox, Cochise County, Arizona area (32°14′16″N; 109°46′15″W; 1279 m asl) in the months of June and July during the years from 1992 to 2017. They were maintained in the laboratory in containers having slightly moistened sandy-loam soil taken from their original habitat, or in gypsum sand. The laboratory temperature ranged from 24–32°C with a relative humidity range from 30–60%.

Laboratory predator-prey tests.—To determine if a velvet mite was an acceptable prey to a variety of vertebrate and arthropod predators, a series of arenas ranging in size from 5 × 8 cm to 36 × 60 cm, depending upon the sizes of the predators, were established. Soil from the original habitat of the mites was used to cover the surface of the arenas. Most of the predators were present in the same habitat as the mites, though others were tested given the widespread occurrence of velvet mites in desert areas around the world.

Tests were conducted by introducing the mite into an arena that already contained the potential predator. In most cases, the interactions were observed until the predator attacked, or had displayed evidence of either avoidance or lack of interest. In some exceptional situations, the animals were left together for longer periods of time. For example, tests involving mites and antlion larvae were conducted in the smallest 5 × 8 cm arenas in which the larva would make a conical pit-trap in the 2.5 cm deep sand. The mite would often fall into the pit, escape, fall in again, and so on, thereby providing the antlion numerous opportunities to catch the mite. In other situations, longer-lasting experiments were performed where the potential predator showed lack of interest. In situations where the predatory behavior was not evident, the predator was provided an alternative, palatable prey and, if that prey item were attacked, the test was scored as no predation.

Chemical defenses.—Velvet mites were analyzed for potential odorous and colored aposematic warning chemicals by extraction into various solvents including cyclopentane, hexane, and methylene chloride (Burdick & Jackson, Muskegon, Michigan, USA) or standard laboratory 95% ethanol. For characterizing the source of the red color in the mites, 64.4 g of mites were immersed in cyclopentane, frozen at -20°C, thawed, and the procedure repeated twice. The extracts were concentrated by rotary evaporation and were chemically analyzed in the laboratory of David Morgan in Keele University, UK.

Detailed characterizations of potential toxic compounds within the body of the mites were not conducted because we observed no symptoms of intoxication by any of the predators that ate some, or all, of a velvet mite. Specifically, we noted lack of any deleterious effects exhibited by antlion larvae that became engorged and turned red after eating a mite.

RESULTS

Most emergences of velvet mites to the soil surface occurred during the month of July or in late June and coincided with the first major rainfall of the summer season and the concurrent flight of reproductive termites (Table 1A). Mass emergences of the mites and the flights of termites, mainly

Table 1A.—Summer rainfall at the Willcox, Arizona research site and the aboveground presence of giant velvet mites.

Date	Rainfall (cm)	Relative abundance of mites	Comments[a]
11 July 1992	3.56	Abundant	First major rainfall
11 July 1993	0.99	Abundant	First major rainfall
30 July 1994	3.43	Abundant	First major rainfall
23 July 1997	2.84	Abundant	First major rainfall
9 July 1998	2.03	Abundant	First major rainfall
27 June 1999	4.32	Abundant	Very localized, first major rainfall
21 June 2001	0.51	One mite	
9 July 2002	<0.25	Very few	
14 July 2004	1.78	Abundant	Very localized, first major rainfall
4 July 2012	1.00	Few	First rainfall
14 July 2017	0.76	Few	First rainfall

[a] A major rainfall is generally considered 1.0 cm or more.

Gnathamitermes perplexus occurred after the nearly 3 months of a dry spring (Table 1B) and the first summer storms that had dropped more than 1 cm of rain (Table 1A). When the first storm delivered 1 cm or less of rain, few mites would surface. For one to three days after the first major storm, the morning sky at the location was typically cloudy and the abundant mites would stay on the surface until the clouds thinned or disappeared. During this time, the mites actively searched the surface of the soil and several times were observed catching and eating reproductive termites (Fig. 2A). The mites were never observed in the field eating non-reproductive termites. In laboratory tests, they would sometimes kill non-reproductives, though they did not feed upon them (Fig. 2B) (J. Cowles, unpub. data).

On 11 July 1992, 2800 velvet mites were captured by aspirator from an area of approximately 2 ha and were divided into size groups of very large, average, and very small. The 85 very large individuals weighed on average 78.7 mg/mite; the 2407 average-sized mites averaged 45.2 mg/mite; and the 308 very small mites averaged 25.5 mg/mite. The average weight of the population was 44.05 mg/mite. Among this population of mites (Fig. 1), 99.5 percent were red with white spots and only 14 individuals were all red with no white spots. Several of the mites were observed molting and leaving the cast exuvia on the soil surface, several were spinning silk into what looked like a mat under the mite that might have been associated with spermatophore deposition (Proctor 1998). Several mites were also in the process of cannibalizing another individual.

Potential predators.—The results of tests in which a variety of predators were offered giant velvet mites as potential prey are summarized in Table 2. Rodents generally investigated the mites, often grabbing them and manipulating them in their mouths before ultimately rejecting them. Two domestic laboratory mice bit and mortally injured mites which were then dropped. Although horned lizards would eat velvet mites, they displayed displeasure with the taste by making mouthing movements that are not seen when eating ants or other prey, and they would eat only one or a few mites before ignoring others. Of the nine other lizard species tested, only three species injured mites with only one species eating a single mite, but not others. Most lizards would either ignore mites outright, lick them and then ignore them, or grab them, sometimes with chewing, before dropping them and ignoring future mites. Toads, like horned lizards, ingest their prey whole and would occasionally consume mites, though they often displayed displeasure in the form of atypical mouthing motions, suggesting an unpleasant taste.

Spiders from five different families and of several feeding strategies all initially attacked velvet mites. Two species of spiders injured mites, but only one tarantula, *Aphonopelma chalcodes* Chamberlin, 1940, of the four tested consumed two mites before rejecting others. Two species of scorpions displayed no interest in the mites. Sun spiders collected on the field site, showed little interest in the mites. An African sun spider grabbed a mite, puncturing it in the process, then dropped it and plowed its mouthparts through the sand. Only one of 29 vinegaroons injured a mite and that vinegaroon did not eat it. Velvet mites were apparently their own worst enemies, given that we observed several times a mite cannibalizing another individual in the field. In contrast, giant centipedes displayed no interest in velvet mites.

Twelve species of predacious insects from four orders exhibited a variety of responses to velvet mites. None of the three species of carabid beetles consumed a mite, though two of the nine *Calosoma* sp. mortally injured and partially ate a mite. Larder beetle larvae (*Dermestes lardarius*), though known as major pests of dried animal specimens in museums, never consumed any parts of mites during several weeks of trials with freshly frozen or dried mites. None of the three mantises offered mites exhibited interest. Likewise, none of the four species of ants displayed predatory interest in the mites even when mites were dropped directly into their nest entrance holes. The ants dragged all mites out of the nest and dropped them outside. Antlions and owlflies (order Neuroptera) are abundant in the sandy area in which the mites were found. The larvae of these insects are well-known for their sickle-shaped

Table 1B.—Average total precipitation (cm), Willcox, Arizona (1898–2005).[a]

Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Year
2.36	2.21	1.65	0.66	0.63	0.96	6.15	6.63	2.97	2.13	1.78	2.77	30.96

[a] Source: https://wrcc.dri.edu/cgi-bin/cliMAIN.pl?azwill

Figure 2.—(A). A velvet mite capturing and feeding upon a reproductive termite. (B). Velvet mite attacking a worker termite. Photographs courtesy of Jillian Cowles.

mandibles and voracious appetites for insects that fall into their conical pits or are encountered by free-roaming species. Natural predation on one mite was observed in the field where the mite was crawling on the soil surface with an antlion larva attached to its leg base. In the laboratory, other antlion larvae, when able to capture a mite, would consume it and turn red. Although adults of these neuropterans appear weak and fragile, they also readily attacked velvet mites but rarely ate them.

Chemical defenses.—Velvet mites have two chemical defenses: warning odor, and offensive taste. The odor is apparent to us and appears to be a pyrazine (G. Jones and D. Morgan, pers. comm.), a member of a well-known group of chemical defenses (Blum 1981). Our own species is a generalist predator that eats a wide variety of animals as food. For this reason, and to grasp an idea of how a mite might taste to other generalists, one of us (JOS) sampled a Willcox mite. After biting the mite with my front incisors, an immediate, overwhelmingly bitter, astringent, and spicy taste exploded throughout my mouth. Within seconds, I spit out the mite and its juices. The chewing never progressed back of my front teeth and the tip of my tongue; nevertheless, the bitterness was detected nearly instantly in the very back of my tongue and lingered for about an hour. To cross-check for bitterness using another species of giant velvet mite, I sampled a fresh mite from Limpopo province of the Republic of South Africa (23°39′51″S; 27°48′35″E; 840 m) – the taste was identical to that of the Willcox mite.

When the contents of two mites were separated from the integument, homogenized, and injected intravenously at a level of 450 mg/kg into a mouse, the animal survived and exhibited no evidence of acute or long-term toxicity. Given this lack of evidence for any toxicity or lethality of the internal tissues of the mites, no further evaluations were conducted.

The red coloration of velvet mites was partially analyzed with solvent extractions. When 20 mites were placed in methylene chloride, the fluid immediately became red. When intact mites were placed in either hexane or 95% ethanol no color was extracted. However, when the mite integument was broken, the red color readily diffused into hexane or ethanol. The color was determined to be from a carotenoid, though the exact chemical structure could not be determined from the sample provided (Graeme Jones, personal communication).

DISCUSSION

The velvet mites in Willcox, Arizona are active only during the summer. In contrast, *D. pandorae*, the best-studied velvet mite species, is active only during the winter in the Mojave Desert of California, where summer rains are rare and most rain falls in the winter (Newell & Tevis 1960; Tevis & Newell 1962). In other regards, the two species shared similarities, including mass emergences of adults after the first major seasonal rains in their geographical area and concurrently with the flights of termites. Both also were noted in the field only preying on reproductive termites, both shunned bright, hot sunlight, both were noted occasionally cannibalizing other individuals, and both were most abundant in areas of sandy soil. The Willcox mites were also present in low numbers after intense summer rains in rocky areas having no apparent sandy areas, a feature not mentioned by Newell and Tevis in their reports (Newell & Tevis 1960; Tevis & Newell 1962).

Velvet mites in the genus *Dinothrombium* possess some of the most effective defenses against predators known. These defenses include aposematic red coloration, aposematic odor, powerful deterrent taste, tough, rubbery integument that resists puncture (Cloudsley-Thompson 1962; Lighton & Duncan 1995), surface activity for only a few hours a year, and synchronized mass emergence of hundreds or thousands of individuals. They do not seem to have internal toxins and their ability to deter predation chemically is apparently solely the result of repugnant taste and unpleasant odors on the integument and possibly in internal tissues. The lack of internal toxins is supported by the observation that antlion larvae, when they were able to puncture the mite, consumed the contents and suffered no apparent ill effects.

Table 2.—Potential predators of giant velvet mites.

Potential predator[a]	Common name	*n*[b]	Not harmed	Injured or eaten[c]	Comments
Vertebrates					
Peromyscus sp. [a]	Deer mouse	1	1		
Feral *Mus musculus*	Mouse	4	4		2 Mites coated with saliva
Lab *Mus musculus*	Mouse	5	3	2	Killed, partially eaten
Meriones unguiculatus	Gerbil	1	1		Sniffed, rejected
Phrynosoma solare	Horned lizard	2	1	1	4 Eaten, mouthed, displeasure
P. cornutum [a]	Horned lizard	1		1	6 Mites eaten over six days
Sceloporus graciosus	Sagebrush lizard	2	1	1	Killed, not eaten
S. jarrovii	Yarrow's lizard	1	1		
S. magister	Desert spiny lizard	1	1		Grabbed, shook, spat out
Aspidoscelis burti	Whiptail lizard	1	1		
Uta stansburiana [a]	Side-blotch lizard	1	1		
Urosaurus ornatus [a]	Tree lizard	15	13	2	1 Licked; 2 chewed and injured
Eublepharis macularius	Leopard gecko	2	2		Shook, rejected, rubbed mouth
Coleonyx variegatus	Banded gecko	3	3		
Anolis sp.	Anole lizard	1		1	Grabbed, dropped, finally eaten
Spea hammondii [a]	Western spadefoot	5	4	1	One toad ate 2 mites
Anaxyrus punctatus	Red-spotted toad	3	1	2	
A. cognatus [a]	Great plains toad	4	1	3	1-3 Eaten, gulping, then rejection
Spiders					
Aphonopelma chalcodes [a] Chamberlin, 1940	Tarantula	4	3	1	Grabbed, dropped, ate 2 mites
Hogna carolinensis [a] (Walckenaer, 1805)	Wolf spider	5	5		Grabbed, dropped
Latrodectus hesperus [a] Chamberlin & Ivie, 1935	Western widow	21	16	5	Silk wrapped, none eaten
Olios giganteus Keyserling, 1884	Giant crab spider	4	3	1	Punctured, then rejected
Araneus diadematus [a] Clerck, 1757	Orb weaver	1	1		Silk wrapped, then cut out of web
Scorpions					
Centruroides sculpturatus ((Wood, 1863)	Bark scorpion	2	2		
Hadrurus arizonensis (Ewing, 1928)	giant hairy scorpion	4	4		
Other arthropods					
Mastigoproctus tohono [a] Barrales-Alcalá, 2018	Vinegaroon	29	28	1	Killed, not eaten
Scolopendra polymorpha [a]	Giant centipede	5	5		
Solpugidae sp. A	Sun spider	2	2		
Galeodes sp. Olivier, 1791	African sun spider	1		1	Grabbed, dropped, plowed through sand
D. magnificum [a] (LeConte, 1852)	Giant velvet mite	+		+	In lab and field seen cannibalizing
Insects					
Myrmeleontidae sp. [a]	Antlion larva	1		1	In field; dragged out of pit still attached
Myrmeleontidae sp. [a]	Antlion larva	10	3	7	In lab; successfully eaten
Myrmeleontidae sp. [a]	Antlion adult	11	3	8	Punctured, not eaten
Ascalaphinae sp. [a]	Owlfly adult	1		1	
Brachinus sp. [a]	Bombardier beetle	1	1		
Calosoma sp. [a]	Ground beetle	9	7	2	2 Punctured, partly eaten
Anthia omoplata	Saber-tooth beetle	1	1		
Dermestes lardarius	Dermestid beetle	2	2		Larvae refused dead mites
Mantodea sp. [a]	Praying mantis	3	3		
Crematogaster sp.	Ants	1	1		Antennated only
Solenopsis xyloni [a]	Southern fire ants	2	2		Dragged out of nest unharmed
Pogonomyrmex rugosus [a]	Harvester ants	7	7		Dragged out of nest unharmed
P. maricopa [a]	Harvester ants	1	1		Dragged out of nest unharmed
Novomessor cockerelli [a]	Long-legged ants	2	2		Dragged out of nest unharmed

[a] Species is present at research site where the mites were collected.

[b] *n* = number of different individual predators tested. Individual predators may be offered more than one mite.

[c] fatal injury or eaten. See comments for explanations.

Few potential predators were observed to prey on velvet mites, and those that did, usually only killed one or few of the individuals and often rejected the partially-eaten mite. Of the vertebrate potential predators, only those that quickly engulf intact prey ate a few mites. These predators included horned lizards and toads. In the field, toads typically would not be potential predators of mites because they are nocturnal and the mites are diurnal. Horned lizards, though diurnal, are present at a relatively low density and eat only a sample of them. This predation would have little effect on populations of mites that often occur in an area by the thousands and share the surface of the ground with ants, termites, and numerous other potential prey species. The one chewing lizard that consumed a single mite was a tree-inhabiting anole that hunts above ground and likely would not risk coming to the ground for a velvet mite. *Dinothrombium magnificum* were also distasteful to fish as were red water mites (Parasitengona: Hydrachnidiae), aquatic relatives of *Dinothrombium* (Proctor & Garga 2004).

No spiders ate a mite, including black widows and orb weavers that in the natural world would not trap mites in their webs. They were tested mainly to demonstrate that mites are unacceptable to spiders, irrespective of whether or not they are likely to encounter the mites in the wild. None of the centipedes or scorpions, vinegaroons, and sun spiders, would consume a mite. Among the tested insect predators, no beetles, ants, or praying mantises would prey upon velvet mites. The only insects that would feed upon mites were antlions and their relatives. These predators would not likely be important because they rarely succeeded in capturing a tough rubbery mite except when the mites were put together in laboratory situations where the antlions had dozens of opportunities to puncture a mite. In the field, most mites would be able to climb out of the antlions' pits and escape.

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