

The paradox of the velvet-ant (Hymenoptera, Mutillidae)

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Abstract

Female diurnal velvet-ants are among the insects most strongly protected against predation. These protections include an exceedingly hard and tightly fitting integument, powerful legs and rapid running ability, aposematic color, aposematic warning stridulation, aposematic odor, and, most famously, legendarily powerful stings. Small to medium-sized velvet-ants were rarely injured or killed in tests against potential predators. Velvet-ant stings are painful, often exceedingly so, but have low toxicity or lethality and are of defensive value primarily by causing intense pain. Despite being well defended against predators they do not form night-time resting aggregations that might enhance mutual protection.

Keywords

Dasymutilla vesta, *Dasymutilla bioculata*, predation, venom, aggregation

Introduction

Velvet-ants are a successful family of more than 4300 species in a large number of subfamilies and genera (Brothers and Lelej 2017). Many female velvet-ants are diurnal, colorful, and highly visible as they rapidly run across the surface of the land. This

[†] Deceased.

makes them conspicuous to a variety of predators including lizards, birds, and an assortment of arthropods and should make them easy prey. Nevertheless, they are rarely observed to be preyed upon. Why is this?

Velvet-ants are also the poster children for uniqueness among the solitary aculeate wasps. Their most conspicuous difference from most other wasps is the total absence of wings in the females and presence of wings in most males (Fig. 1). Other unusual properties of females are the possession of an extremely hard and tight-fitting integument compared to other solitary wasps, their exceedingly strong legs, their generally “furry” body covered with dense setae, their possession of stridulatory organs capable of producing a loud signal that is readily audible to humans and presumably many other predators (Schmidt and Blum 1977), and their unusually long adult lifespan (Evans and Miller 1969; Schmidt 1978). Finally, and perhaps most importantly, female velvet-ants have the longest stinger relative to body size of any aculeate hymenopteran (Sadler et al. 2018) (Fig. 2). This extraordinarily long stinger of females (males have no stinger, like all male aculeates, because the stinger is a modified ovipositor) fits into the wasp’s metasoma by uniquely curling like an old-fashioned watch spring towards the anterior of the metasoma then curving and returning back to exit at the tip of the metasoma (Fig. 3), as described by Hermann (1968). In conjunction with the long stinger, velvet-ants are renowned for their ability to deliver painful stings to victims who happen to grasp them (Mickel 1928; Rice 2014; Schmidt 2016; Jensen et al. 2021). This ability to induce extreme pain has resulted in their common name of “cow killer” (Mickel 1928; Rice 2014). One of the largest species, *Dasymutilla occidentalis* (Linnaeus, 1758), was extensively tested against a large number of potential predators and found to be nearly devoid of predators (Schmidt and Blum 1977), though the species was later found to have one predator that was sometimes successful (Vitt and Cooper 1988). Gall et al. (2018) reported that velvet-ants are considered to have few, if any, predators.

The paradox of velvet-ants is why they are dramatically different from other wasps in the Vespoidea, despite being nestled deeply within the clade (Brothers 1999, 2019). They range in body length from about 2 mm to 25 mm and come in a dazzling variety of colors and combinations including red, orange, yellow, silver,

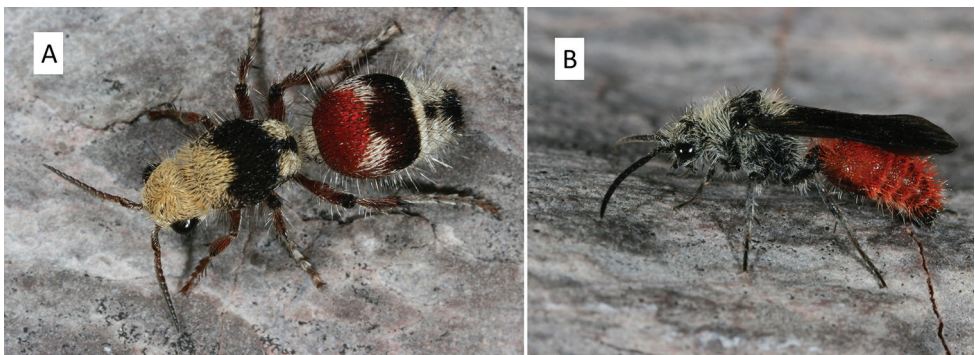


Figure 1. *Dasymutilla asteria* Mickel, 1936. **A** female **B** male. Photos by Jillian Cowles.



Figure 2. *Dasympulilla vesta* (Cresson, 1865) showing the length of the stinger. Photo by Justin Schmidt.

white, and black. Many species are aposematic and form mimicry rings and complexes (Wilson et al. 2015). Aposematic species of insects often form aggregations for mutual protection (Cott 1940), including aggregations of mixed species (Edmunds 1974). So far as we know, the question of potential aggregation for mutual defense among female velvet-ants has not been explored in the literature. We address this question here using two species, explore the effectiveness of the defenses of small to medium-sized velvet-ants against several potential predators, and evaluate velvet-ant venom toxicity to mammals.

Materials and methods

Challenges with potential predators

Velvet-ants were collected in southern Georgia and north and central Florida, USA during the summer of 1976. They were returned to the lab and housed in containers with a layer of sand on the bottom and provided honey and water *ad lib*. To determine if a velvet-ant were an acceptable prey to a variety of predators, a series of arenas with sandy floors was established. These ranged in size from 5×8 cm to 36×60 cm, depending upon the sizes of the predators. Tests were conducted by introducing the velvet-ant into an arena that already contained the potential predator. In most cases, the interactions were observed until the predator attacked or had displayed either avoidance or

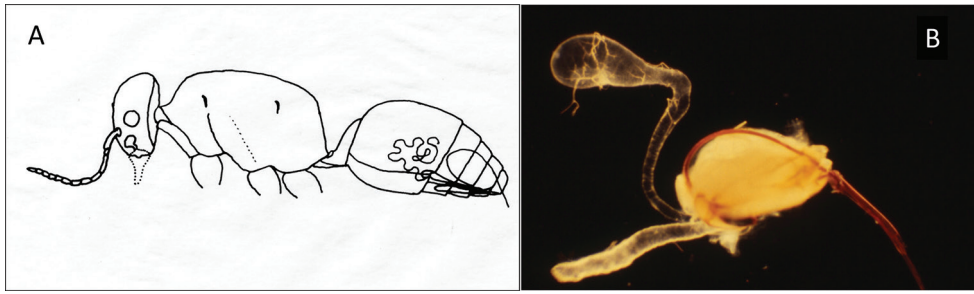


Figure 3. **A** drawing illustrating how the sting shaft coils within the velvet-ant metasoma **B** dissection showing the large venom reservoir (top) and smaller tubular Dufour's gland (bottom) connecting to the base of the sting shaft. Illustration and photograph by Justin Schmidt.

lack of interest. In some exceptional situations the animals were left together for longer periods of time. For example, tests involving velvet-ants and antlion larvae were conducted in the smallest 5×8-cm arenas in which the larva would make a conical pit-trap in the sand. The velvet-ant would often fall into the pit and escape from it repeatedly, thereby providing the antlion numerous opportunities to catch it. In situations where the predatory behavior was not evident, the predator was then provided an alternative, palatable prey and, if that prey item were attacked, the test was scored as no predation on the velvet-ant.

Measurement of sting pain and lethality

Because sting pain cannot readily be measured instrumentally or with great precision, a pain scale for the immediate, acute pain caused by a sting was developed (Schmidt et al. 1984; Starr 1985). The scale ranges in values from 1 – 4 and is based upon a value of 2 assigned to the sting of a honey bee (*Apis mellifera* Linnaeus, 1758). Painfulness of stings received in the field while working with velvet-ants was compared to stings previous received from honey bees. If the pain of the velvet-ant sting was considerably less than that of a honey bee sting, it was rated as a 1; if about the same as a honey bee sting, then a 2; and if substantially more painful than a honey bee sting, then a 3.

To determine the lethality of the venom of velvet-ants, pure venom was obtained by the method of Schmidt (2019). In brief, frozen velvet-ants were thawed, their sting apparatuses removed to a spot of distilled water, the venom reservoir (minus filamentous glands) was pinched off at the duct and removed from the rest of the sting apparatus, twice rinsed with distilled water, and placed in a clean approximately 50 µl droplet of distilled water. The venom was then squeezed from the reservoirs and the empty chitinous reservoirs were discarded. The pure venom was lyophilized and stored at -20 °C until used. For lethality tests dried venom in saline was injected either intravenously or intraperitoneally into mice and recorded as LD₅₀ measured as mg venom/kg of body weight (Schmidt 2019).

Potential formation of overnight resting aggregations

An arena 60×60×4 cm LWH with washed grey sand to a depth of 7 mm and covered with a clear glass top was established in the laboratory in Athens, Georgia. The top edge faced the single window that provided natural sunlight. Refugia within the arena were 6×8-cm rectangles of 80-lb weight index-card material placed on top of the sand in the four corners, midway along the four sides, and with a final rectangle placed in the center of the arena. Thirty-six female *Dasymutilla vesta* (Cresson, 1865) collected in Union County, Florida and 12 female *D. bioculata* (Cresson, 1865) (Williams et al. 2011) collected in Burke County, Georgia were introduced into the arena on 28 September 1976. Honey and water on adjacent 2-cm squares of aluminum foil were positioned at $\frac{1}{4}$ and $\frac{3}{4}$ along diagonals between the opposite corners of the arena. The velvet-ants wandered freely within the arena and choose at nightfall to take refuge under one of the rectangles or to bury themselves in the open sand. Each morning around sunrise they were surveyed for their positions underneath the rectangles or in a location in the sand. The sand was smoothed to become uniform again and the individuals were free to continue their daily activities and choose again where to spend the next night. The procedure was replicated 11 times. The results were analyzed by chi-square tests with Yates correction for the number of observed individuals located under the rectangles during the entire experiment with the expected value based on equal randomness at all nine positions, as determined by dividing the entire number of individuals under the combined rectangles by nine to yield an expected value for each individual rectangle.

Results

Potential predators

The outcome of challenges in which a very small, *Pseudomethoca frigida* (Smith, 1855) (4–6 mm long (Brothers 1972)), small, *Dasymutilla vesta* (6–10 mm), or medium-sized *Pseudomethoca sanbornii* (Blake, 1871) (8–14 mm), velvet-ants were introduced into an arena containing a predator are listed in Table 1. In almost all cases when a velvet-ant was grabbed, she could be heard and seen stridulating while extruding and retracting her stinger. Some predators abandoned the attack upon the commencement of the stridulation; others would persist irrespective of the stridulation. For example, gerbils, Florida scrub lizards, and various unidentified spiders often ceased the attack when the velvet-ant stridulated, whereas antlion larvae appeared unaffected by the stridulation.

Most gerbils would release velvet-ants as soon as the latter stridulated. Some, however, persisted and two out of six individuals attacking *D. vesta* were stung and dropped their velvet-ant, only to grab her again, this time rapidly spinning her with the paws while biting. This action appeared to prevent further stings, allowing the velvet-ant to be consumed. Two of the gerbils that avoided velvet-ants after their initial encounters

Table 1. Trials of potential predators of small to medium-sized female velvet-ants.

Potential predator (Common name)	Velvet-ant species	n [†]	Result [‡]	Comments
Vertebrates				
<i>Meriones unguiculatus</i> (gerbil)	<i>Dasymutilla vesta</i>	6	2+,4–	Grabbed, stung, released, repeat, eaten
<i>M. unguiculatus</i>	<i>D. vesta</i>	2	2–	Stinger experimentally removed; naïve gerbil grabbed and released; experienced gerbil avoided
<i>Mus musculus</i> (mouse)	<i>D. vesta</i>	4	4–	Minor interest, could not hold wasps
<i>Sceloporus woodi</i> (Florida scrub lizard)	<i>D. vesta</i>	2	2–	Grabbed, released, no further attacks
<i>S. woodi</i>	<i>D. vesta</i>	3	3–	Stinger removed; grabbed, released
<i>S. woodi</i>	<i>Pseudomethoca frigida</i>	2	1+,1–	Ate 3 <i>P. frigida</i> , avoided <i>D. vesta</i> ; the other lizard avoided <i>P. frigida</i>
<i>Anolis carolinensis</i> (Carolina anole)	<i>D. vesta</i>	1	1–	Stinger removed; eyed, but no attack
Spiders				
<i>Aphonopelma hentzi</i> (tarantula)	<i>Pseudomethoca sanbornii</i>	11	1+,10–	148 mg spider ate; 10 spiders 163–363 mg could not puncture
<i>A. hentzi</i>	<i>D. vesta</i>	11	9+,2–	Spiders 148–363 mg
<i>A. hentzi</i>	<i>D. vesta</i>	9	9–	Adult spiders; some grabbed, none injured
<i>Hogna carolinensis</i> (wolf spider)	<i>P. sanborni</i>	5	5–	Adult spiders
Insects				
Myrmecoleontidae sp. (antlion larvae)	<i>D. vesta</i>	3	3–	Repeatedly grabbed but could not hold
Myrmecoleontidae sp.	<i>P. frigida</i>	4	1+,3–	3 Grabbed but could not puncture; 1 ate

† n = number of different individual predators tested.

‡ + = velvet-ant eaten; – = velvet-ant not injured or eaten.

also the next day avoided velvet-ants whose stingers had been clipped to eliminate their ability to sting.

Florida scrub lizards avoided *D. vesta* irrespective of whether they had an intact stinger or not. In contrast, one lizard attacked and consumed three of the much smaller *P. frigida*. The one tested Carolina anole did not attack a *D. vesta* that had her stinger clipped.

Most small immature tarantulas (Areaneae:Theraphosidae) attacked, but did not succeed in injuring, the medium-sized *P. sanbornii*. Those same small tarantulas overwhelmed most of the smaller *D. vesta*. For unknown reasons, all nine adult tarantulas did not prey on their offered *D. vesta*.

Larval antlions readily grabbed and attempted to puncture offered velvet-ants. Only one individual succeeded in piercing and consuming a *P. frigida*, a much smaller species than *D. vesta*.

Sting pain and venom lethality

The sting pain level of most small velvet-ants such as *Dasymutilla vesta*, *D. asteria* Mickel, 1936, *D. thetis* (Blake, 1886), *D. archboldi* Schmidt & Mickel, 1979, and *P. frigida* was a 1 on the pain scale. Larger species including *D. bioculata*, *D. gloriosa* (Saussure, 1868), *D. foxi* (Cockerell, 1894) and *D. sicheliana* (Saussure, 1868) delivered a pain level of 2. Stings of the largest species such as *D. klugii* (Gray, 1932) were intensely painful and rated a level of 3. Sting pain levels of 3 are uncommon and is

observed in only a few other species including harvester ants in the genus *Pogonomyrmex* and a few large paper wasps in the genus *Polistes* (Schmidt 2016). All stings by velvet-ants, irrespective of size or pain intensity, differed qualitatively from stings received by honey bees, social wasps, and ants in that they produced a rashy-itchy sensation much like that of stinging plant nettles. The sensation elicited an intense urge to rub the sting site. The rubbing did not diminish the pain which continued noticeably for 15 minutes or more. Compared to stings of honey bees and social wasps, velvet-ant stings produced no red puncture spot with a white surrounding area and only minimal flare or swelling.

The published values for the venom lethality of *D. klugii* is 70 mg/kg (Schmidt 2019) and for *D. bioculata* (as *lepeletierii*) is 75 mg/kg (Schmidt et al. 1984). In addition to these values, when the venom of *Pseudomethoca simillima* (Smith, 1855) was injected intraperitoneally into a mouse at a dose of 76 mg venom/kg mouse, the animal survived. The lethality of the venom of *D. bioculata* (as *pyrrhus*) based on three mice was 86 mg/kg. The most lethal of the velvet-ant venoms was that of *D. occidentalis* at 32 mg/kg based on two mice. Overall, the venom of five species in two genera of velvet-ants is only marginally lethal to mammals compared to venoms of most social Hymenoptera.

Overnight resting locations

The overnight resting locations of *D. vesta* and *D. bioculata* are shown in Table 2. The average number of *D. vesta* seeking overnight refuge under the individual card rectangles for the combined 11 days of replication ranged from 2.09 to 4.27. Only one position yielded a highly significant fewer number of individuals than expected. When the four corner rectangles are combined, the number of *D. vesta* residing under them was not different from expected ($\chi^2 = 0.07$, $P = \text{ns}$). In contrast, the four mid side rectangles when combined had marginally more individuals residing under them than expected ($\chi^2 = 4.23$, $P < 0.05$).

The resting locations for *D. bioculata* were based on 10 replicates because on one day the survey was too late and many of the individuals were already active on the surface and that replicate was excluded. The results were similar to those of *D. vesta* in that significantly fewer individuals were found under the center rectangle than expected. Likewise, the combined four corners sheltered no different number of individuals than expected ($\chi^2 = 2.85$, $P = \text{ns}$). The combined four mid side rectangles sheltered marginally more individuals than expected ($\chi^2 = 6.05$, $P < 0.05$).

To determine if the two species interacted with each other positively or negatively, the results of the 10 replicates in which both species were present at the same time were combined and analyzed (Table 2). Again, the combined four corners were not different from expected ($\chi^2 = 0.46$, $P = \text{ns}$). The four mid sides sheltered more individuals than expected ($\chi^2 = 7.42$, $P < 0.01$). The center rectangle sheltered far fewer individuals than expected ($\chi^2 = 15.85$, $P < 0.001$). This pattern indicated that behaviors of the two species were independent and did not affect each other.

Table 2. Total of velvet-ants seeking overnight refuge in each location[†].

Location	Light Lf corner	Light mid	Light Rt corner	Left mid	Dark Lf corner	Dark mid	Dark Rt corner	Right mid	Center	Sand
<i>Dasymutilla vesta</i> (replicated 11 times)										
Total	40	40	37	37	32	47	39	46	23	50
Mean	3.64	3.64	3.36	3.36	2.91	4.27	3.55	4.18	2.09	4.55
S Dev	2.06	2.38	2.11	1.43	1.30	1.19	1.69	2.09	1.51	1.69
Chi sq	0.14	0.14	0.01	0.01	1.53	4.94	0.02	3.06	10.93	n/a
Prob	ns	ns	ns	ns	ns	0.05	ns	ns	0.005	n/a
<i>Dasymutilla bioculata</i> (replicated 10 times)										
Total	9	11	10	15	7	13	10	12	2	30
Mean	0.9	1.1	1.0	1.5	0.7	1.3	1.0	1.2	0.2	3
S Dev	0.74	0.74	1.70	1.65	0.48	0.95	1.63	1.55	0.42	1.41
Chi sq	0.03	0.08	0.00	4.30	1.15	1.38	0.00	0.52	11.04	n/a
Prob	ns	ns	ns	0.05	ns	ns	ns	ns	0.001	n/a
Both species combined (replicated 10 times)										
Total	44	45	45	49	36	55	45	54	25	76
Mean	4.4	4.5	4.5	4.9	3.6	5.5	4.5	5.4	2.5	7.6
S Dev	2.27	2.42	2.84	1.37	1.17	1.43	2.17	1.78	1.51	1.71
Chi sq	0.00	0.00	0.00	0.83	2.70	4.78	0.00	3.89	15.85	n/a
Prob	ns	ns	ns	ns	ns	0.05	ns	0.05	0.001	n/a

[†] Abbreviations: Light=side facing window; Dark=furthest side from window; Lf=arena left side when looking toward window; Rt=arena right side when looking toward window; corner=intersection of any two sides; mid=middle of any side; Center=center of the arena; Sand=any open sand space in the arena.

Discussion

Female velvet-ants of all sizes appear to have few significant predators. The relatively small sized *Dasymutilla vesta* survived most attacks by gerbils, especially if they managed to sting the attacker. Gerbils are rodents that readily prey on insects and small invertebrates. Some gerbils learned from the encounter with *D. vesta* to avoid the species in a later encounter, even when the velvet-ant had been rendered harmless by modification of the stinger. Gerbils are intelligent predators and some learned to avoid stings by quickly rotating the insect with their paws while biting to inactivate her, a behavior that likely would also be useful in their native desert habitats of Asia where they are presumed to encounter stinging scorpions.

Florida scrub lizards grabbed *D. vesta*, then quickly released them unharmed. This apparently was not because of the sting as individuals incapable of stinging were also quickly released. Although Florida scrub lizards damaged no *D. vesta*, they did overwhelm three of the much smaller *Pseudomethoca frigida*. This might be because the integument of the smaller *P. frigida* was not as hard and could be crushed in the lizards’ jaws.

Spiders presented a mixed story. Some tarantulas could overcome and consume velvet-ants, whereas others would not attack them. Large wolf spiders (Lycosidae) would attack and then release velvet-ants. This appears to be the result of the vibration transmitted to the spider’s chelicerae by the stridulation of the velvet-ant (Schmidt and Blum 1977).

Antlion larvae are omnipresent in the sandy areas frequented by velvet-ants in this study and could present serious risks. Despite falling into their conical pits numerous times in our tests, no *D. vesta* was ever successfully captured and eaten by a larva. One *P. frigida* that was grabbed was punctured and eaten. In the case of antlion larvae, the velvet-ants' integumental hardness and the tight-fitting sclerites appear to be the key to their survival.

Despite their common name of "cow killers", the stings of velvet-ants are not especially toxic to mammals. The most lethal venom of the five species evaluated was estimated 32 mg/kg for *D. occidentalis*. This lethality pales in comparison to those of the honey bee at 2.8 mg/kg, or 0.4 mg/kg for *Pogonomyrmex* harvester ants (Schmidt 2019). Apparently, the velvet-ant's "bark" is much greater than her "bite" and even a large number of their stings certainly could not kill a cow.

Velvet-ants are frequently encountered in good habitats in large numbers (Mickel 1928; Manley and Taber 1978; Schmidt and Hook 1979). Nevertheless, they are generally considered solitary insects that do not cluster or aggregate. High densities of velvet-ants in relatively small areas would provide ideal conditions for them to form aggregations for mutual protection as occurs with other aposematic, noxious, and/or well-defended species. We are unaware of any literature reports that velvet-ants form resting aggregations during either hot times of the day or at night. For this reason, we tested the hypothesis that, when given the opportunity, they might form overnight resting aggregations. Our results indicate that female velvet-ants of the two tested species do not form overnight resting aggregations when provided ample opportunities; rather, individuals randomly select sites for spending the night irrespectively of other individuals. The only exception to the lack of randomness was observed in the center refugium which contained significantly fewer individuals than expected. This is consistent with individuals attempting to leave the arena to find suitable locations and they randomly chose locations at the edges of the arena, simply because they were prevented from going further. We have no strong explanation for the marginally significantly higher number of individuals under the refugia placed at the mid sides and suspect that this occurred by chance. We also did not observe any positive or negative interactions between the two species when selecting overnight resting positions.

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