Stinging wasps (Hymenoptera: Aculeata), which species have the longest sting?

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The stings of bees, wasps, and ants are something that catches the attention of anyone that experiences them. While many recent studies have focused on the pain inflicted by the stings of various stinging wasps, bees, or ants (Hymenoptera: Aculeata), little is known about how the length of the sting itself varies between species. Here, we investigate the sting length of a variety of aculeate wasps, and compare that to reported pain and toxicity values. We find that velvet ants (Hymenoptera: Mutillidae) have the longest sting compared to their body size out of any bee, wasp, or ant species. We also find that there is no link between relative sting length and pain; however, we did find an inverse relationship between relative sting length and toxicity with taxa having shorter relative stings being more toxic. While we found a significant relationship between host use and relative sting length, we suggest that the long sting length of the velvet ants is also related to their suite of defenses to avoid predation.
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Abstract

The stings of bees, wasps, and ants are something that catches the attention of anyone that experiences them. While many recent studies have focused on the pain inflicted by the stings of various stinging wasps, bees, or ants (Hymenoptera: Aculeata), little is known about how the length of the sting itself varies between species. Here, we investigate the sting length of a variety of aculeate wasps, and compare that to reported pain and toxicity values. We find that velvet ants (Hymenoptera: Mutillidae) have the longest sting compared to their body size out of any bee, wasp, or ant species. We also find that there is no link between relative sting length and pain; however, we did find an inverse relationship between relative sting length and toxicity with taxa having shorter relative stings being more toxic. While we found a significant relationship between host use and relative sting length, we suggest that the long sting length of the velvet ants is also related to their suite of defenses to avoid predation.
Introduction

Hymenoptera (ants, bees, and wasps) have likely been of interest to humans for as long as we have existed. Our histories are tied closely together with Hymenoptera. Paleolithic paintings depicting bees have been found dating from 15,000 years ago in the caves of Spain, and pottery vessels used for beekeeping have been found dating from 9,000 years ago (Piek 1986; Roffet-Salque et al. 2015). However, as we have sought out honey and wax for our own benefit during the Meso- and Neolithic, we also were undoubtedly introduced to bee’s defensive stings. While colloquially many refer to the “stinger” of bees, wasps, and ants, among entomologists the correct term both for the stinging structure (the noun) and the action (the verb) is simply “sting” and as entomologists we will refer to the structure as such. For example, it would be correct to say “the bee was able to sting me with her sting” rather than “…sting me with her stinger.” Bees, ants, and many of the more familiar wasps fall within an infraorder of Hymenoptera called Aculeata, which is defined by the modification of the egg laying device (ovipositor) into a sting apparatus. Among the aculeates, the use of the sting is primarily for prey capture or host paralysis, and defense. While people often associated stings with bees, many wasps, and ants have even more painful stings than bees (Schmidt 2016).

Hymenoptera venom is the most potent of any of the animal venom (Schmidt 1990a). An estimated 100 deaths per year can be attributed to stinging Hymenoptera, which is 3-4 times the number of deaths that occur by snake bites (Schmidt 1986a). However, with the exception of allergic reactions, most people only experience temporary pain and edema. In fact, an adult human could safely withstand 1,000 bee stings (Fitzgerald & Flood 2006). It is estimated that a
lethal dose does not occur until a threshold of 20 stings/kg (Fitzgerald & Flood 2006). Although the result of a large number of stings may not be death, pain is a certainty.

As many of us have experienced, the amount of pain that bee and wasp stings cause varies by species. Yet for some reason, a bee sting (generally the sting of a European honey bee, Apis mellifera) has become somewhat of a benchmark for pain. A shot at the doctor’s office, for example, is often equated to a “quick sting, no worse than a bee.” Starr (1985), with the later expansion by Schmidt (1990a) and Schmidt (2016), created a pain scale that opens the topic of sting pain up to a more general audience. This method ranks pain on a scale that varies from one, which is the least painful, and includes small sweat bees (Lasioglossum spp.) and native fire ants (Solenopsis geminata), to four, which is the most painful, and includes the bullet ant (Paraponera clavata) and tarantula hawks (Pepsis spp.) (Schmidt 2016).

Pain from wasp envenomation can come from two sources with the first being from the chemical composition of venom itself. Hymenoptera venom can be two forms, alkaloid and proteinaceous (Blum 2012; Schmidt et al. 1986). Hymenoptera venoms are known to vary in toxicity as given by studies of LD_{50} (a measure of lethality) and enzymatic activity. Schmidt et al. (1980) found that the LD_{50} of various aculeate wasps varied from 0.25 mg/kg to 71 mg/kg with harvester ants (Pogonomyrmex spp.) having the most toxic venoms and velvet ants (Dasymutilla klugii) and the German hornet (Paravespula germanica) having the least toxic of the venoms. Schmidt et al. (1986) found that aculeate venom also varies in eight different enzymes with species of velvet ants (Dasymutilla lepeletierii) once again having some of the lowest of the enzymatic activities.

The second cause of pain is due to mechanical damage from the sting puncturing tissue. Spider wasps (Pompilidae) and velvet ants seem to be paradoxical having a high pain rating, but
a low LD$_{50}$ and weak enzymatic activity (Schmidt 1986a; Schmidt 2004; Schmidt et al. 1980). Observations have been made that the wasps having the highest pain indices on the Schmidt and Starr Pain Scale (Schmidt 1990a; Schmidt 2016; Starr 1985) are often those with the largest bodies. The reason that these wasps cause intense pain may be due to the morphology of the sting itself. Much attention has been paid to the chemical components of venom, but little has been done concerning the morphology of the sting, and specifically its relative length. While comparisons of ovipositor length have been done for parasitoid wasps (Townes 1975), no comparisons have been made among the stinging wasps, the aculeates.

In this study we investigate the relative length of the stings of various aculeate wasps and compare these lengths to known measures of toxicity, enzyme activity, and pain. A particular focus is given to the velvet ants (Mutillidae), because they are known to not only have a painful (yet relatively harmless) sting, but also, they are known to have an exceptionally long sting (Schmidt 2016) (Fig. 1a).

**Methods**

**Sting length**

The stings were measured for species from 14 families of aculeates (including ants and bees) (Table 1). All specimens were sourced from the Department of Biology Insect Collection at Utah State University (EMUS). The sting from each specimen was dissected and photographed using a Leica camera and microscope with light dome; calibrations were checked prior to any photographs. Measurements were taken from the tip of the lancet along the curve of the sting shaft to the beginning of the triangular plate using Image J (Rasband et al. 2011). In order to obtain a relative measure of sting length to body size, the mesosomal length was
measured as a proxy to overall body length. Because position of the head varies from specimen
to specimen, and the gaster can be expanded or contracted depending on the specimen, total body
lengths are difficult to determine and are not consistent from one individual to another. While
various proxies have been used to estimate body length of Hymenoptera, including head width
(Haggard & Gamboa 1980), intertegular distance (Greenleaf et al. 2007), and wing length (Bosch
& Vicens 2002), proxies associated with wings could not be used, as not all aculeates have wings
(i.e., ants and velvet ants). We selected the mesosoma as a proxy for body length, as it is not
moveable and can easily be measured in preserved specimens. For a consistent measurement the
mesosoma was measured form the anterior apex of the pronotal flange to the dorsal margin of the
propodeal foramen in lateral view. Multiple images of each specimen were taken using a Leica
camera with light dome. All images were then combined using Zerene Stacker v1.04, and
measurements were made (based on 1mm scale bar) using Image J (Rasband et al. 2011).

Measurements were made in replicate depending on if the species was common. For
common species, stings were extracted from five individuals and measurements of both the sting
and the mesosoma were made for each specimen. These are indicated in Table 1 by those
individuals with a standard deviation (STD) for both sting measurements and mesosomal length
measurements. Because sting dissection is a destructive process, only a single specimen was
extracted in instances where a species was rare. These species are indicated on Table 1 by those
individuals without STD for either sting measurements or mesosomal length measurements

We also wanted to make use of the extensive slide collection of aculeate stings at the
Department of Biology Insect Collection at Utah State University (EMUS). However, most
stings previously slide mounted had no associated voucher specimen, likely due to the
destructive nature of sting extraction. To make use of these slides and avoid the destruction of
additional museum specimens, for those species where a slide-mounted sting was available we selected five individuals of that same species from the EMUS collection and the mesosomal lengths were measured for these specimens. The largest and smallest specimens were measured, and a range of sizes between were chosen to represent a continuum. These are indicated in Table 1 by those individuals with STD for only the mesosomal length measurements.

In addition to the sting measurements and mesosomal length measurements, we also calculated a relative sting length based on a ratio of the sting length to the mesosomal length.

Toxicity, pain, and host preference

Measures of host preference, toxicity, and pain were derived from the literature (Brothers & Finnamore 1993; Schmidt 1986a; Schmidt 1986b; Schmidt 1990a; Schmidt 2004; Schmidt 2016; Schmidt et al. 1980; Schmidt et al. 1986; Starr 1985). Toxicity measures were only available for a handful of species (Table 1). For some species (e.g., Polistes apaches), toxicity measures were only available for closely related species within the same genus. In these cases we averaged the published toxicity of other members of the genus to estimate an average toxicity for these taxa. This averaging was only done at the genus level, so taxa without toxicity measures for other members of their genus were not included in the toxicity vs. sting length analyses.

While measuring pain from insect stings is undoubtedly a subjective endeavor, recently the “Schmidt pain index” has received much attention as it attempts to compare the pain of various Hymenoptera stings using a scale of 1-4, 1 being low pain and 4 being high (Schmidt 2016). Unfortunately, in addition to the pain rankings being subjective, they are generally not assigned to specific species, but rather given as a range for a taxonomic group (e.g., velvet ants, small species get a pain ranking of 1-2, but no species identifications are given for these “small species” (Schmidt 1990a)). To account for the lack of species-level measures of pain, we
assigned each species we had a measure of sting length an estimated pain value based on the
actual value for related species (when known). In many wasp families no measures of pain have
been published, so for these instances we assigned potential pain values based on closely related
wasp families and personal experience. Linear regression was used to compare the relative sting
length to pain estimates.

Data Analysis. For the situations where there were multiple measurements for a given
species, these measurements were then averaged and standard deviations were calculated (Table
I).

To investigate what factors were associated with the sting length, we used an ANCOVA
with sting length as the response variable and mesosomal length, wasp type (velvet ant or other
wasp), and the interaction between mesosomal length and wasp type as the predictor variables.
Furthermore, we used linear regression to compare sting length to various other measures.
Toxicity measures (though only available for a subset of species) and pain estimates were
individually compared to the relative sting length (sting length/mesosomal length) with relative
sting length as the response variable, and either the pain estimates or the toxicity as the predictor
variables. Sociality was also compared to relative sting length with relative sting length as the
response variable and sociality (either social or solitary) predictor variables. Similarly sociality
was compared to pain with pain being the response variable and sociality as the predictor
variable. To determine if any trends existed in host choice, host data was compared to relative
sting length with relative sting length as the response variable and host as the predictor variable.
All analyses were computed using R (RDevelopment CORE TEAM 2008).

Results

Sting length
Of the 21 species of velvet ants measured, the actual sting length ranged between 3.3 mm and 13.5 mm with *Dasymutilla occidentalis* having the longest sting. The relative sting length varied, but was above 1 for all velvet ants with a species of *Dasylabris* from Russia having the longest relative length. Of the 39 non-velvet ant wasps measured, the actual sting length varied between 1 mm and 14.3 mm with the relative sting length being below 1 for all but a few species (Table 1). *Pepsis* sp. had the longest overall sting length (14.33 mm) though the relative sting length was 1, indicating that the overall length was likely related to the large size of the wasp. Velvet ants had a much larger relative sting length compared to most other wasps, with an outlying wasp, *Sapyga elegans*, grouping with the velvet ants (Fig. 1b).

We found a significant positive relationship between mesosomal length and sting length \((F_{2,57} = 111.2; R^2 = 0.796, P < 0.0001)\) for both velvet ants and other aculeates (Fig. 1b). Additionally we found that there was a significant difference between velvet ants and other aculeates \((F_{2,57} = 111.2; R^2 = 0.796, P < 0.0001)\). While both velvet ants and other aculeates show a positive relationship between mesosoma length and sting length, the significant interaction \((F_{3,56} = 107.7; P < 0.0001)\) between velvet ant and non-velvet ant datasets indicates that velvet ants sting length increases significantly more as the velvet ants body size increases compared to all other aculeates (Fig. 1b).

While we did find a significant positive relationship between overall sting length and pain \((F_{1,58} = 18.75; R^2 = 0.2443, P < 0.001)\), indicating that larger wasps generally have a more painful sting, we found no relationship between relative sting length (sting length compared to the mesosomal length) and pain \((F_{1,58} = 0.2682; R^2 = 0.0046, P =0.6065)\). Furthermore, we found marginally significant evidence that toxicity was inversely related to sting length \((F_{1,7} = 5.175; R^2 = 0.425, P =0.05707)\), indicating that aculeates with longer stings relative to their body.
size were less toxic than those with smaller stings relative to their body size (Fig. 2). Also, as has previously been suggested (Schmidt et al. 1980; Schmidt et al. 1986), we found no significant relationship between venom lethality and reported pain of the sting ($F_{1,7} = 1.212; R^2 = 0.1476, P =0.3073$). We did, however, find a weakly significant relationship between sociality and relative sting length ($F_{1,58} = 4.383; R^2 = 0.07026, P =0.04068$), with social species having shorter stings relative to their bodies than solitary species. We found no relationship, though, between sociality and pain ($F_{1,58} = 2.848; R^2 = 0.04681, P =0.09685$).

We found that the species’ ecology, the host/prey use in particular, was significantly correlated to relative sting length ($F_{10,49} = 19.49; R^2 = 0.7991, P <0.0001$) with those taxa that use immature Hymenoptera as their host having significantly longer stings compared to their bodies than all other aculeates (Fig. 3). These include all of the velvet ants and the sapygid wasp (a close relative of velvet ants (Branstetter et al. 2017)).

**Discussion**

Our results show that there is no link between relative sting length and pain. It should be mentioned that measuring the pain associated with stings is a subjective endeavor and these measures should be viewed as soft assessments rather than hard metrics. Regardless, while one might assume the longer stings would inflict more pain, based on personal observation, when someone is stung by an aculeate wasp, the sting only shallowly penetrates the skin. This observation suggests that the sting length is not used to inject venom deeper into the victim, but likely has been selected for other purposes (discussed below). While sting length does not seem to be associated with pain, we did find an inverse relationship between relative sting length and toxicity (though only a limited number of taxa could be included in the analysis), with taxa
having shorter relative stings being more toxic. This could be related to the way different taxa use their stings. Most wasps use the sting to immobilize or kill their host (Schmidt 2016). There is some necessity, therefore, for these wasps to evolve venoms that are toxic enough to effectively immobilize their prey. Velvet ants, on the other hand, parasitize hosts (immature hymenoptera) that are already immobile, and it has been suggested that their sting and associated venom is primarily used for defense (Schmidt 2016). Highly toxic venom for defense might be selected against, as it would be more beneficial for a velvet ant to inflict pain, but not mortally wound a potential predator facilitating learned avoidance, which has been demonstrated in feeding trials with various vertebrates (Gall et al. in press).

Our results clearly show that velvet ants have the longest stings out of the stinging wasps in relation to their body size (Fig. 1a,b). For example, the velvet ant *Dasymutilla occidentalis* had a sting nearly as long as the tarantula hawk (*Pepsis* sp.) that was twice its size (Table 1). Some velvet ant species have been given the common name of “cow killer” (Schmidt 1990b), which are theoretically named because anyone who was stung would claim it hurt bad enough to “kill a cow” (Schmidt 2016). This ominous common name, however, is somewhat enigmatic given that velvet ants have some of the least toxic venoms of any of the wasps (Schmidt 1986b; Schmidt et al. 1980; Schmidt et al. 1986). While velvet ants have the longest sting (compared to their body) out of any aculeate, their stings are, however, short compared to many parasitic wasps. One of note being *Euurobracon yokohamae*, which has an ovipositor 7.7 times the length of the body (Townes 1975).

It is not entirely clear why velvet ants have such long stings, yet the fact that sting length is correlated to host type suggests something about their parasitic nature has driven the evolution
of exceptionally long stings. Below, we will explore two potential hypotheses that might explain
the size of the velvet ant sting.

First, the long sting of velvet ants might help them immobilize their host in the tight
confines of the host nest cell. While little is known about the behavior of velvet ants when they
are in their host nest, it is clear that these wasps are parasitic primarily on immature bees and
sphecid wasps, generally parasitizing the prepupa or pupal stage of their host (Brothers &
Finnamore 1993). Most velvet ants parasitize solitary, ground nesting species (Brothers &
Finnamore 1993). To successfully parasitize a host, the parasite must find the host nest, open the
host nest cell (either underground or in a pre-existing cavity), and oviposit near the host prepupa
or pupa. From the few descriptions of velvet ant parasitism behaviors it appears that the adult
velvet ant opens the nest cell only enough to allow her head access, permitting her to probe the
nest cell with her antennae to determine if the host has finished consuming its provision
(indicating the nest cell is appropriate for oviposition) (Brothers 1972). Once an appropriate nest
cell is identified, the female velvet ant will turn around and insert the tip of the metasoma into
the opening in the wall of the nest cell and probe around with her sting (Brothers 1972). The
female velvet ant will sting the host only if it is in the pupal stage, but will simply oviposit if the
host is in the prepupal stage with the sting apparently serving to stop development of the host
(Brothers 1972; Janvier 1933). It is possible that the long sting of the velvet ants enhances their
ability to parasitize the host in the close confines of an underground nest cell.

This hypothesis, however, does not seem to be supported in other wasps. Scoliid wasps,
for example, also parasitize ground nesting hosts, specifically beetle larvae (Brothers &
Finnamore 1993). While they undoubtedly also face similar challenges to the velvet ants in
finding a host and paralyzing it with a sting in the tight underground burrow of the beetle, yet
scoliids do not have a long sting. This suggests that other factors, other than the tight confines of
the host underground nest might be playing a role in the selective advantage of the length of the
velvet ant’s sting.

A second hypothesis regarding the length of velvet ant sting is that it evolved in response
to predation pressures. Velvet ants are among the most highly defended of all stinging wasps
(Manley 2000; Schmidt 2016; Schmidt & Blum 1977). These defenses include aposematic
coloration, stridulation (auditory aposematism), pungent exudate secretions, a hard cuticle, and a
painful sting (Manley 2000; Schmidt 2016; Wilson et al. 2012). Not only do velvet ants have the
longest stings (as our results clearly show), they also have one of the most flexible and
maneuverable apical metasomal segments enabling them to reach their sting to nearly every part
of their body (Schmidt 2016). Because velvet ant’s hosts are largely immobile, they are thought
to only rarely sting their prey (Schmidt 2016), instead it has been suggested their sting is
primarily used to defend against predators (Schmidt & Blum 1977). In fact, the length of the
sting, combined with the hard cuticle of the velvet ants makes them nearly indestructible (Vitt &
Cooper 1988).

Several of the more unique aspects of the velvet ant sting and venom make them highly
effective against predators. First, as is mentioned above, the length and agility of the sting,
combined with their extraordinarily hard cuticle, aposematic coloration, and stridulation enables
velvet ants to quickly and effectively train predators to avoid them. Gall et al. (in press), for
example, found that when a lizard (in this study the lizard was Aspidoscelis tigris) attacks a
velvet ant, it is unable to crush it because of the hard cuticle, as the lizard attempts to manipulate
the velvet ant in its mouth, the velvet ant is quickly able to sting the lizard. Once released, the
aposematic coloration of the velvet ant apparently facilitates rapid learning in the lizard. In many
instances after experiencing the sting of a velvet ant (and the other defenses) a lizard will not
attempt to attack another velvet ant, even with over a year between exposures to these wasps
(Gall et al. in press). The second aspect of velvet ant stings and venom chemistry that make them
highly effective predatory deterrents is the mildly toxic, but highly painful sting. This enables
velvet ants to train predators with a painful sting, but the mild toxin does no lasting damage.
The highly effective defenses of velvet ants, of which the long sting plays a key role,
have enabled velvet ants to diversify around the world. Furthermore, these defenses have been
influential in the evolution of the world’s largest known Müllerian mimicry complex among
diurnal velvet ants (Wilson et al. 2015; Wilson et al. 2018; Wilson et al. 2012).

Conclusions

Our study of the sting length of various bees, wasps, and ants finds that velvet ants have
the longest sting compared to their body size out of any aculeate. While there was no link
between relative sting length and the pain associated with the sting, we did find an inverse
relationship between relative sting length and toxicity, with taxa that have shorter relative stings
being more toxic. While we found a significant relationship between host use and relative sting
length, we suggest that the long sting length of the velvet ants may also be related to their suite
of defenses to avoid predation.

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Figure Legends

Figure 1. Sting length vs. mesosomal length among aculeates. (a) Dasymutilla calorata with her sting extended showing its length. (b) Graph of mesosomal length vs. sting length. Velvet ants are indicated in black and other aculeates in grey. Regression lines are indicated. Examples of various velvet ants and other aculeates are also pictured.

Figure 2. Graph of relative sting length versus toxicity. Relative sting length is negatively correlated to toxicity. Relative sting length is a ratio of the sting length/mesosomal length and toxicity is measured in mg/kg with lower numbers being more toxic. Velvet ants are marked with black and other aculeates are marked with grey.

Figure 3. Relative sting length compared to host preferences. Relative sting length is significantly correlated to host use in those wasps that parasitize immature Hymenoptera, but not in all other aculeates. (a) Boxplot showing relative sting length vs. host use. (b) Scatter plot of sting length vs. mesosomal length (see Fig. 1) with taxa colored based on host preferences.
Table 1 (on next page)

Aculeate taxa included in analyses.

Sting and mesosomal lengths are given in mm and relative sting length is a ratio of sting length/mesosomal length. Sociality, host data, toxicity, and pain are derived from the literature (Brothers & Finnamore 1993; Schmidt 1986a; Schmidt 1986b; Schmidt 1990a; Schmidt 2004; Schmidt 2016; Schmidt et al. 1980; Schmidt et al. 1986; Starr 1985). Toxicity data were not available for all taxa, but where possible, toxicity data for closely related species (within the same genus) was averaged for the genus and included in the table (e.g., *Polistes*). Similarly, pain data were not available for all taxa, but estimated pain values were included based on reported pain values, personal observation, or known pain indices from related taxa.
Table 1. Aculeate taxa included in analyses. Sting and mesosomal lengths are given in mm and relative sting length is a ratio of sting length/mesosomal length. Sociality, host data, toxicity, and pain are derived from the literature (Brothers & Finnamore 1993; Schmidt 1986a; Schmidt 1986b; Schmidt 1990a; Schmidt 2004; Schmidt 2016; Schmidt et al. 1980; Schmidt et al. 1986; Starr 1985). Toxicity data were not available for all taxa, but where possible, toxicity data for closely related species (within the same genus) was averaged for the genus and included in the table (e.g., *Polistes*). Similarly, pain data were not available for all taxa, but estimated pain values were included based on reported pain values, personal observation, or known pain indices from related taxa.

| Family       | Species                        | Sting | STD | Mesosoma | STD | Relative sting length | Sociality | Prey/host | Toxicity (LD50 mg/kg) | Pain |
|--------------|--------------------------------|-------|-----|----------|-----|-----------------------|-----------|------------|-----------------------|------|
| Rhopalosomatidae | *Rhopalosomatidae nearcticum* | 2.15  | 3.29| 0.65     | solitary | Grylloptera | 1 |
| Vespidae     | *Vespa crabro*                | 5.39  | 0.28| 9        | 0.57| 0.6      | social    | Predator   | 2.9               | 2    |
|              | *Polistes apachus*            | 3.81  | 0.52| 6.44     | 0.45| 0.59     | social    | Predator   | 3.7               | 2.5  |
| Tiphiiidae   | *Tiphia sp. 1*                | 3.66  | 4.71| 0.78     | solitary | Coleoptera | 1 |
|              | *Tiphia sp. 2*                | 2.7   | 0.45| 5.54     | 0.69| 0.49     | solitary | Coleoptera | 1                |      |
| Chyphotidae  | *Typhoctes peculiaris*       | 3.06  | 3.07| 1        | solitary | Unknown  | 1 |
|              | *Chyphotes mandibularis*     | 2.28  | 3.38| 0.67     | solitary | Unknown  | 1 |
|              | *Chyphotes albipes*          | 1.26  | 0.24| 1.67     | 0.31| 0.75     | solitary | Unknown  | 1                |      |
|              | *Chyphotes belfragei*        | 1.83  | 0.3 | 2.83     | 0.47| 0.65     | solitary | Unknown  | 1                |      |
| Thynnidae    | *Methoca stugia*             | 2.89  | 2.18| 1.32     | solitary | Coleoptera | 1 |
|              | *Diamma bicolor*             | 3.87  | 8.19| 0.47     | solitary | Coleoptera | 3 |
|              | *Anthobosca sp.*             | 2.1   | 2.69| 0.78     | solitary | Coleoptera | 1 |
|              | *Myzinum sp.*                | 4.73  | 5.43| 0.87     | solitary | Coleoptera | 1 |
| Pompilidae   | *Anoplius (Notiochares) lepidus* | 5.49  | 9.1 | 0.6      | solitary | Spiders  | 2.5 |


| Family                  | Species                      | Length | Width  | Height | Larval Stage | Order                     | Abundance |
|------------------------|------------------------------|--------|--------|--------|--------------|---------------------------|-----------|
| Anopliinae             | Anoplius (Pompilinus) insolens | 3.39   | 4.72   | 0.72   | solitary     | Spiders                   | 2.5       |
|                        | Aporus luxus                 | 4.37   | 5.41   | 0.81   | solitary     | Spiders                   | 2.5       |
|                        | Ageniella blaisdelli         | 2.69   | 3.84   | 0.7    | solitary     | Spiders                   | 2.5       |
|                        | Entypus unifasciatus         | 4.74   | 8.43   | 0.56   | solitary     | Spiders                   | 2.5       |
|                        | Évagetes sp.                 | 2.07   | 3      | 0.69   | solitary     | Spiders                   | 2.5       |
|                        | Pepsis sp.                   | 14.33  | 14.35  | 1      | solitary     | Spiders                   | 65        |
|                        | Tachypompilus sp.            | 4.66   | 9.08   | 0.51   | solitary     | Spiders                   | 2.5       |
|                        | Sericopompilus sp.           | 4.31   | 5.24   | 0.82   | solitary     | Spiders                   | 2.5       |
|                        | Arachnospila arctus          | 3.54   | 4.82   | 0.73   | solitary     | Spiders                   | 2.5       |
|                        | Anoplius (Arachnophroctonus) chiapanas | 3.96 | 5.14 | 0.77 | solitary | Spiders | 2.5 |
| Sapygidae              | Sapyga elegans               | 4.89   | 1.64   | 3.61   | 0.39         | Immature Hymenoptera      | 1         |
| Myrmosidae             | Myrmosa unicolor             | 2.41   | 2.21   | 1.09   | solitary     | Coleoptera                | 1         |
| Mutilidae              | Atillium jucundum            | 8.1    | 5.24   | 1.55   | solitary     | Immature Hymenoptera      | 2         |
|                        | Cephalomutilla haematodes    | 4.85   | 2.98   | 1.63   | solitary     | Immature Hymenoptera      | 2         |
|                        | Dasylabris sp.               | 7.84   | 3.38   | 2.32   | solitary     | Immature Hymenoptera      | 2         |
|                        | Dasymutilla gloria          | 9.11   | 4.68   | 1.94   | solitary     | Immature Hymenoptera      | 2         |
|                        | Dasymutilla nigripes         | 5.96   | 3.14   | 1.9    | solitary     | Immature Hymenoptera      | 2         |
|                        | Dasymutilla occidentalis     | 13.52  | 0.98   | 7.42   | 0.54         | Immature Hymenoptera      | 71        |
|                        | Ephuta bellus                | 3.34   | 1.92   | 1.74   | solitary     | Immature Hymenoptera      | 1         |
|                        | Hoplomutilla phoreys         | 9.31   | 6.86   | 1.36   | solitary     | Immature Hymenoptera      | 2         |
|                        | Hoplomutilla xanthocerata    | 11.91  | 8.08   | 1.47   | solitary     | Immature Hymenoptera      | 2         |
| Family          | Genus          | Species                       | Body Length  | Wing Length | Length Without Wings | Life Stage | Order   | Category          | MQ | Degree |
|-----------------|----------------|-------------------------------|--------------|-------------|-----------------------|------------|---------|------------------|----|---------|
| Mutillinae      | Mutillina sp.  | 6.69                          | 5.03         | 1.33        | solitary              | Hymenoptera | 1.5     |                  |    |         |
|                 | Myrmilla       | erythrocephala                | 4.01         | 3.44        | 1.16                  | Hymenoptera | 1.5     |                  |    |         |
|                 | Pertylella      | haracioi                      | 4.83         | 3.35        | 1.44                  | Hymenoptera | 1.5     |                  |    |         |
|                 | Pristomutilla  | sp.                           | 4.1          | 3.08        | 1.33                  | Hymenoptera | 1.5     |                  |    |         |
|                 | Pseudomethoca  | sanbornii                     | 5.98         | 3.49        | 1.71                  | Hymenoptera | 1.5     |                  |    |         |
|                 | Pseudophotopsis| komarovii                     | 6.85         | 4.94        | 1.39                  | Hymenoptera | 1.5     |                  |    |         |
|                 | Sigilla        | dorsata                       | 4.46         | 3.14        | 1.42                  | Hymenoptera | 1.5     |                  |    |         |
|                 | Smicromyrme    | viduata                       | 9.25         | 4.51        | 2.05                  | Hymenoptera | 1.5     |                  |    |         |
|                 | Sphaerothalamapensylvanica | 7.55          | 4.13        | 1.83                  | Hymenoptera | 2       |                  |    |         |
|                 | Stenomutilla   | argentata                     | 5.77         | 2.85        | 2.02                  | Hymenoptera | 2       |                  |    |         |
|                 | Timulae        | grotei                       | 5.69         | 0.3         | 3.54                  | Hymenoptera | 2       |                  |    |         |
|                 | Tramautomutilla| sp. Paraguay                  | 10.44        | 6.27        | 1.67                  | Hymenoptera | 3       |                  |    |         |

**Bradyrhaenidae**

| Family          | Genus          | Species                       | Body Length  | Wing Length | Length Without Wings | Life Stage | Order | Category | MQ | Degree |
|-----------------|----------------|-------------------------------|--------------|-------------|-----------------------|------------|-------|----------|----|--------|
|                 | Apterogyna     | sp.                           | 2.36         | 1.93        | 1.22                  | solitary   | Unknown |          |    |         |
|                 | Bradyrhaenaeus | sp.                           | 2.02         | 1.93        | 1.05                  | solitary   | Unknown |          |    |         |

**Scoliidae**

| Family          | Genus          | Species                       | Body Length  | Wing Length | Length Without Wings | Life Stage | Order   | Category | MQ | Degree |
|-----------------|----------------|-------------------------------|--------------|-------------|-----------------------|------------|---------|----------|----|--------|
|                 | Scoliia        | dubia dubia                   | 5.06         | 8.9         | 0.57                  | solitary   | Coleoptera |          |    |         |
|                 | Camposomerus   | tolteca                       | 4.59         | 0.4         | 7.2                   | solitary   | Coleoptera | 63 | 1 |        |

**Formicidae**

| Family          | Genus          | Species                       | Body Length  | Wing Length | Length Without Wings | Life Stage | Order | Category | MQ | Degree |
|-----------------|----------------|-------------------------------|--------------|-------------|-----------------------|------------|-------|----------|----|--------|
|                 | Paraponera     | clavata                       | 4.89         | 0.14        | 6.32                  | social     | Predator | 6      |    |        |
|                 | Solenopsis     | invicta                       | 0.77         | 0.12        | 1.31                  | social     | Predator | 1      |    |        |

**Crabronidae**

| Family          | Genus          | Species                       | Body Length  | Wing Length | Length Without Wings | Life Stage | Order   | Category | MQ | Degree |
|-----------------|----------------|-------------------------------|--------------|-------------|-----------------------|------------|---------|----------|----|--------|
|                 | Bicyrtes       | caprioptera                   | 4.23         | 5.22        | 0.81                  | solitary   | Hemiptera | 1      |    |        |
|                 | Sphecia        | speciosus                     | 9.38         | 11.49       | 0.82                  | solitary   | Hemiptera | 46 | 1.5 |        |
|                 | Oxybelus       | argentipilosus                | 1.09         | 1.66        | 0.66                  | solitary   | Diptera   | 1      |    |        |
|                 | Astata         | bakeri                        | 1.74         | 3.73        | 0.47                  | solitary   | Hemiptera | 1      |    |        |
| Family   | Species            | Length (mm) | Width (mm) | Height (mm) | Color Code | Diet                  | Number |
|----------|--------------------|-------------|------------|-------------|------------|-----------------------|--------|
| Apidae   | Apis mellifera     | 2.99        | 0.13       | 4.69        | 0.39       | social Herbivore       | 2      |
| Apidae   | Xylocopa virginica | 5.02        | 0.44       | 7.81        | 0.64       | solitary Herbivore     | 22     |

**Bembix amoena**

- Length (mm): 4.46
- Width (mm): 0.24
- Height (mm): 6.98
- Color Code: 0.39
- Diet: Diptera
- Solitary: 0.64

**Apis mellifera**

- Length (mm): 2.99
- Width (mm): 0.13
- Height (mm): 4.69
- Color Code: 0.39
- Diet: Herivore
- Social: 0.64

**Xylocopa virginica**

- Length (mm): 5.02
- Width (mm): 0.44
- Height (mm): 7.81
- Color Code: 0.64
- Diet: Herivore
- Solitary: 0.64
Figure 1

Sting length vs. mesosomal length among aculeates.

(a) *Dasymutilla calorata* with her sting extended showing its length. (b) Graph of mesosomal length vs. sting length. Velvet ants are indicated in black and other aculeates in grey. Regression lines are indicated. Examples of various velvet ants and other aculeates are also pictured. Photo credit: Joseph S. Wilson.
Figure 2

Graph of relative sting length versus toxicity.

Relative sting length is negatively correlated to toxicity. Relative sting length is a ratio of the sting length/mesosomal length and toxicity is measured in mg/kg with lower numbers being more toxic. Velvet ants are marked with black and other aculeates are marked with grey.

*Note: Auto Gamma Correction was used for the image. This only affects the reviewing manuscript. See original source image if needed for review.*
Figure 3

Relative sting length compared to host preferences.

Relative sting length is significantly correlated to host use in those wasps that parasitize immature Hymenoptera, but not in all other aculeates. (a) Boxplot showing relative sting length vs. host use. (b) Scatter plot of sting length vs. mesosomal length (see Fig. 1) with taxa colored based on host preferences.
