

Chapter 2

Entomological Aspects of Insect Sting Allergy

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To provide a biological framework for understanding stinging insects, a basic taxonomic review is warranted. All stinging insects belong to the order Hymenoptera, which translates as “membrane winged.” This order is divided into two suborders: the Symphyta (sawflies and horntails) whose members are considered more primitive and are completely incapable of stinging, and the Apocrita which includes the more advanced taxa with many groups capable of stinging. The Apocrita is comprised of two groups, the first being the Terebrantes (previously known as Parasitica) many of which, as their name suggests, typically parasitize other insects and are of considerable economic benefit. Only a few taxa in the Terebrantes are capable of a weak poking of their ovipositor. The remaining group is the Aculeata which include all the true stinging forms—the ants, bees, and “true” wasps. This is the group that will be addressed in this chapter, even though some members have secondarily reduced stings rendering them incapable of stinging (e.g., some ants, as pointed out below). Figure 2.1 illustrates the taxonomic placement of the families having the greatest allergenic importance.

Both social and solitary members of the Aculeata sting as a means of individual defense, such as when bodily movement is restricted by being held or squeezed, but social species also “volunteer” to sting when their colonies are disturbed or damaged. Although field experience will generally teach one as to what circumstances will elicit stinging and what behavioral signs indicate that stinging is imminent, most patients are not in a position (or desire the opportunity!) to gain such knowledge firsthand (though a traumatic incident may have led to their becoming venom allergy patients in the first place and stimulate a vicarious interest in learning more about the offending insect). However, there are ways to minimize the likelihood of stings which will be addressed for the respective taxa discussed below.

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Phylogeny of Stinging Hymenoptera

Class Insecta (all insects)

Order Hymenoptera (all ants, bees, wasps, sawflies, horntails)

Suborder Symphyta (sawflies and horntails)

Suborder Apocrita (ants, bees, and “narrow-waisted” wasps)

[group] Terebrantes (Parasitica) (solitary, mostly non-stinging wasps)

[group] Aculeata (ants, bees, stinging wasps)

Superfamily Apoidea (bees)

Family Apidae (honey bees, bumble bees, carpenter bees)

Family Halictidae (sweat bees)

[additional families]

Superfamily Vespoidea (ants and most wasps)

Family Formicidae (“true” ants)

Family Mutillidae (velvet “ants”)

Family Pompilidae (spider wasps)

Family Vespidae (hornets, yellow jackets, paper wasps, etc.)

[additional families]

Fig. 2.1 Phylogeny of stinging Hymenoptera

Only the female insects are capable of stinging, and their sting apparatus has been described in detail [1]. Male genitalia possess “claspers” which are used in mating and are harmless although the insects typically go through threatening motions if held and will often protrude their genitalia. In the case of social species, females may be either workers or queens, and for many taxa the queens, which are capable of stinging, generally use their stings only for individual defense. In exceptional situations “foundresses,” initiating a new colony, will attack and sting if their small nests are disturbed. Of course the queen honey bee is well known for her intolerance of rival queens, resorting to stinging such rivals, but otherwise will rarely sting even if held.

One of the most important taxonomic families within the Aculeata is the family Formicidae which comprises the ants. Within the ants are about 16 recognized

subfamilies, not all of which are capable of stinging. For example, the subfamily Formicinae, also known as the formicine ants, defend by biting and spraying formic acid at their enemies. Two well-known members of this subfamily are the large and conspicuous carpenter ants (genus *Camponotus*) that usually build their nests in wood, and the somewhat smaller mound-building ants of the genus *Formica*. The formic acid-releasing abilities of these ants can be demonstrated easily by grabbing a worker ant and smelling the acid exuded from the ant's abdomen (a procedure not recommended for ant-allergic individuals). The genera responsible for most medically important stings in the United States are not in the Formicinae but within the subfamilies Myrmicinae and Ponerinae. The Myrmicinae includes the most important stinging genus—*Solenopsis* or fire ants.

Ants are native to all continents except Antarctica, and are also found on most large islands. All ants are social, meaning that they live in colonies having one or more queens (or in a few cases only specialized workers that are physiologically and behaviorally like queens). The workers are sexually underdeveloped females that normally do not lay eggs but are responsible for the other tasks within the nest, such as obtaining food, nest building, feeding the larvae, and defending the nest. Queens and male ants (the latter having been reared from haploid eggs due to parthenogenesis, as is normally the case with all the Hymenoptera) possess wings, while workers are always wingless. In contrast, the queens have wings attached in such a way that they are easily removed. Ant colonies generally reproduce by “swarming” in that when the season and weather conditions are suitable, males and new queens of a given species rush forth from the colony and fly away. Other colonies of the same species in an area also swarm, facilitating cross-mating. After the males have mated, their life span is limited, and they often fall prey to other insects, spiders, etc. The newly mated queens land, remove their wings, and then find a small cavity in which to initiate a new colony. These queens of most species do not forage for food—they use the resources stored in their wing muscles to produce and regurgitate food for the larvae that hatch from the first eggs they lay (all the species within the order Hymenoptera have four life stages: egg, a grub-like larva, a mummy-like pupa, and finally the adult stage). Eventually a small group of undersized workers appears, and they forage for food to nourish the queen and larvae, such food often being living or dead insects, depending upon the species of ant. Thus, the colony grows as more workers are produced, and eventually males and new queens are reared. Ant colonies can live for several years, so the same colony can release swarms several times over the course of its duration. Some species may have less than a hundred adults in a colony, while others may have well over 100,000 [2].

Although there are several species of fire ants, the two most important species in the United States are introductions from South America, which include the red imported fire ant (*Solenopsis invicta* Buren) (Fig. 2.2) and the black imported fire ant (*Solenopsis richteri* Forel), sometimes abbreviated as RIFA and BIFA, respectively. (Zoological names are composed of a genus and a species (both italicized), plus the name(s) of one or more authors who originally described the species, the latter not being italicized. The generic name may be abbreviated after the first usage for a given species. If a taxonomic revision has placed the species into another

Fig. 2.2 *Solenopsis invicta* (imported fire ant) workers. https://upload.wikimedia.org/wikipedia/commons/9/94/Fire_ants_01.jpg ([Origin: Stephen Ausmus; Image Number K11622-1; <http://www.ars.usda.gov/is/graphics/photos/dec04/k11622-1.htm> Image K11622-1.jpg “Fire ants”] 1058 × 1890 pixels. Photo in public domain per ARS-USDA website)



genus since the original description, the author's name is placed within parentheses; otherwise, no parentheses are used. If a subspecies is being cited, the author of the subspecies is used rather than the name of the original describer of the species.) In spite of their names, these ants are both brown, though *S. richteri* is much darker, and typically has a lighter area on the abdomen, while *S. invicta* is more uniformly chestnut brown. Although the black species was the first of the two to be introduced into the United States via Mobile, AL in 1918 from South America, it has been largely displaced by the red species (introduced in the early 1930s) [3], causing its range to essentially be restricted to eastern Mississippi and western Alabama. The two species do not interbreed in their native continent, but hybridization takes place in their new home, with *S. richteri* losing ground to *S. invicta* both literally (geographically) and genetically (pure *S. richteri* is becoming scarce), and *S. invicta* remains the dominant species from Central Texas eastward to and throughout Florida, and northward through eastern North Carolina, with outlying introductions. The species is also established in Puerto Rico [4, 5]. There is evidence that the hybrid ants have greater physiological resistance to freezing temperatures [6], which

may allow their range to extend northward, including the southern tiers of counties in Tennessee. These are small ants, with workers being from about 3–5 mm in length, and having clubbed antennae. Both species of *Solenopsis* and their hybrids build mounds sometimes a foot or more in height, and both the mounds and the ground under them contain numerous tunnels and chambers essential for providing a suitable temperature for the brood being reared in the nest. Additional background information about the biology of imported fire ants can be found in Rhoades 1977 [7]. Although tunnels radiate from each mound underneath the soil surface, the mounds themselves have no obvious entrances; however, any disturbance to a mound, especially if the surface is broken, results in a frenzy of workers that rush out to attack and sting the intruder. Envenomization is achieved by each ant fastening to the enemy's body with its mandibles and then stinging one or more times, sometimes making a circle of wounds. If sufficient venom is injected, a sterile pimple-like pustule will form within a day [8]. One can pick up individual fire ant workers between the finger tips without being stung because the stinging apparatus is so small that the ant must brace itself with its mandibles and position its sting to be successful (again, a procedure not recommended for those who are hypersensitive). Most other stinging insects cannot be held safely in this manner.

The native fire ant species—the southern fire ant *S. xyloni* McCook, the tropical fire ant *S. geminata* (Fabricius), which has both small and large workers, with the latter having oversized heads, and the tiny light-colored desert fire ant *S. aurea* Wheeler—are occasionally responsible for anaphylactic reactions [9, 10]. Their colonies are smaller than those of the imported species, and they are generally less aggressive. Where the imported species overlap their ranges, the native species have become less abundant [10]. Stings from fire ants can generally be prevented by learning to recognize their mounds and avoiding them; this is addressed in greater detail below.

In addition to fire ants, two other genera of ants are of some importance in the United States due to their stings: the harvester ants (*Pogonomyrmex*) (Fig. 2.3), and the imported Asian needle ant *Brachyponera chinensis* (Emery) (Fig. 2.4) previously known as *Pachycondyla chinensis* (Emery).

Fig. 2.3 *Pogonomyrmex* (harvester ant) worker. https://upload.wikimedia.org/wikipedia/commons/6/6a/Pogonomyrmex_badius_casent0103057_profile_1.jpg ([Photographer: April Nobile/from AntWeb.org CC-BY-SA-3.0 CASENT0103057] 1037 × 808 pixels. License: Attribution-Share Alike Creative Commons License)



Fig. 2.4 *Brachyponera chinensis* (Asian needle ant) worker. https://upload.wikimedia.org/wikipedia/commons/a/a0/Brachyponera_chinensis_casent0104738_profile_1.jpg ([Photographer: April Nobile/from AntWeb.org CC-BY-SA-3.0 CASENT0104738] 1037 × 808 pixels. License: Attribution-Share Alike Creative Commons License)



Harvester ants are found in the drier areas of the western United States and adjacent Canada, with one species (*P. badius* (Latreille), the Florida harvester ant) extending across the Gulf States to the East Coast. Other species are found in Mexico and Central and South America. They are relatively large ants, and at least in the case of the Florida harvester ant, the largest workers have particularly enlarged heads to house the muscles and mandibles needed for biting through the seeds the ants gather and store in their nests. Colonies are easily recognized by their large mounds (rather flat in some species) that have a distinct bare area around them caused by the ants' chewing off the vegetation; these mounds may exceed 4 ft in diameter. Although the species vary as to their defensiveness, their venoms are the most toxic insect venoms currently known (based upon LD50 in mice) [11, 12] and in humans tend to cause a throbbing pain that spreads to the lymph nodes. Anaphylaxis caused by harvester ant stings has been reported by Klotz et al. [9]. As with fire ants, preventing stings from harvester ants is best achieved by avoiding their nests.

The Asian needle ant (*B. chinensis*), as the name suggests, is an introduction from eastern Asia (from Japan and Korea to Vietnam, the Philippines, and Thailand) initially collected on the East Coast of the United States in 1932, in the Norfolk, VA, area and was soon found to be well established in eastern North Carolina, eventually being reported as far west as Tennessee. This species is approximately the same size as a larger fire ant worker but has a more "cylindrical" shape (particularly in the gaster or continuous portion of the abdomen) and one "hump" or segment in the petiole (in contrast to the two found in fire ants and harvester ants) connecting the thorax with the gaster typical of the ponerine subfamily. They are omnivores though apparently preferring termites as food. Needle ants are not aggressive but will sting if squeezed against the flesh. A description of the local effects of their sting from the "School of Ants" website mentions an immediate slight burning sensation followed by spreading of the painful area to about an inch diameter and remaining sensitive for about 2 weeks [13]—however, published reports indicate variable local effects [14]. Anaphylaxis has been documented in Korea (e.g., Klotz et al. [9]) and in the United States [15]. Needle ant nests are small and inconspicuous. Stings are best

avoided by inspecting outdoor objects before picking them up and by wearing gloves while gardening or otherwise working with soil and objects in contact with soil.

Other notorious ants of the world include the “bullet” ants (*Paraponera clavata* (Fabricius)—a ponerine species) of South America and southern Central America, known for their extremely painful stings, and the “bull” ants of Australia (various species of *Myrmecia*, particularly the aggressive *M. pilosula* F. Smith commonly known as the “jack jumper” ant); the stings of the latter genus are responsible for anaphylactic reactions in addition to pain. (The genus *Myrmecia* belongs to the subfamily Myrmeciinae, which is different from the subfamily Myrmicinae in spite of the similar name.)

Vespidae

The members of most families of aculeate wasps are solitary. The family Vespidae is an exception that contains both truly social and solitary species. Solitary species do not live in colonies or have a worker caste, but typically a single female mates, seeks appropriate food such as prey that is paralyzed by a sting, and stocks her small nest with this prey and then abandons the nest after laying one or more eggs. Regardless of whether they are solitary or social, most aculeate wasps are capable of stinging, with some of solitary members known for their painful stings (e.g., the wingless “velvet ants” or “cow killers” of the family Mutillidae sometimes seen crawling on the ground, especially in sandy areas, and the large tarantula hawks of the genus *Pepsis* (in the family Pompilidae commonly seen in the southwestern deserts and whose sting earns the highest rating of 4 on the Schmidt sting pain index)) [14]. However, the real culprits causing mass stinging or anaphylactic reactions in this family are not the solitary species, but the social species.

Within the family Vespidae are several subfamilies—a few being solitary while others are social. The largest colonies in the temperate regions of the Northern Hemisphere are built by members of the all social subfamily Vespinae which includes the genera *Vespula*, *Dolichovespula*, *Vespa*, and the nocturnal genus *Provespa*. In the United States and Canada, the first two genera are responsible for most stings from this subfamily. One of the many species of *Vespa* has been introduced to North America from Europe, while the three species of *Provespa* are strictly from tropical and subtropical areas of southern and southeastern Asia with none having become established elsewhere; therefore, the latter genus will not be addressed further here.

The life cycles of the various vespine species are similar. An individual overwintered queen becomes active in the spring and builds a small nest of paper mainly from chewed wood pulp containing perhaps a dozen cells, depending upon the species and circumstances. An egg is laid in each cell, and after each hatches, the queen collects animal protein, usually by predation, and feeds each larva. The queen also collects wood pulp to enlarge the nest, including lengthening the cells to accommodate the growing larvae, and protects the nest. After the larvae mature, become

pupae, and emerge as adults, the newly emerged workers gradually replace all the functions the queen has been performing except egg laying. The nest continues to grow, and a large population of workers is reared. Usually around late summer or autumn, stingless males and new queens are reared. (Some researchers prefer to call the young females “gynes”—reserving the word “queen” until the female insect initiates a new colony.) At this time, males and new queens mate (generally from different colonies), the old queen dies, the workers gradually die off, the males leave and succumb to cold weather or predators, and the newly mated queens seek a location to hibernate. The cycle is repeated the following spring when the new queens become active again.

The genus *Vespula* contains two distinct groups of species, with the appropriate taxonomic placement of a smaller third group still subject to differences of opinion. The first group, often called the *V. vulgaris* group but sometimes referred to by European researchers as *Paravespula* [16], include species that produce large colonies whose workers fulfill most of the their brood’s need for protein by scavenging which, in addition to their tendency to be abundant, leads to frequent encounters with people and thus stinging incidents. Some members of this group have been successful in colonizing new areas; for example, *V. pensylvanica* (de Saussure) has become established in Hawaii, *V. vulgaris* (Linnaeus) is now abundant in New Zealand, and *V. germanica* (Fabricius) has colonized much of the United States in addition to southern South America, South Africa, and many other regions. Members of this group native to North America include the widespread and common eastern *V. maculifrons* (du Buysson), the somewhat more restricted eastern *flavopilosa* Jacobson, and the widespread *alascensis* (Packard) restricted to cooler regions, the last species having been recently recognized as distinct from the true *V. vulgaris* native to the Old World [17]. These three native species along with *V. vulgaris* (Fig. 2.5), which resemble each other rather closely, build nests frequently containing a couple thousand adults and use decayed wood such as a rotting stump as their

Fig. 2.5 *Vespula vulgaris* worker. https://upload.wikimedia.org/wikipedia/commons/9/9b/Flying_Vespula_vulgaris.jpg ([Photographer: Soebe] 715 × 635 pixels. License: GNU Free Documentation License)



Fig. 2.6 Nest of *Vespula vulgaris*. https://upload.wikimedia.org/wikipedia/commons/e/e6/Vespula_germanica_nest_-_Zoo_Frankfurt.jpg ([Original photo misidentified as *Vespula germanica* nest; photographer JuTa] 1976 × 1680 pixels. License: Creative Commons Attribution-Share Alike 3.0 Unported)



pulp source. The resulting nest is comprised of brittle paper the color of sawdust (Fig. 2.6). Nests are typically, but not always, constructed underground. Each nest begins with an individual overwintered queen selecting a location, such as a rodent burrow or a space remaining from a decayed tree root, and building a golf ball-sized nest containing a dozen or so cells. She lays an egg in each cell and rears the first brood of workers that, in turn, take over most activities of collecting pulp and expanding the nest, procuring food, and defending the nest. This allows the queen to focus on egg laying. The nest of a mature colony often exceeds the size of a volleyball and contains five to perhaps a dozen combs. Cells used for rearing queens, built later in the season, are much larger than those that produce workers and males, with entire combs in the lower portion of the nest dedicated to rearing new queens. Combs of vespine wasps are oriented horizontally within the nest, and the single layer of cells in each comb opens downward. The oldest comb, with a distinct center core representing the queen mother's original endeavors, is at the top, and each successive comb is built underneath it. The combs are used strictly for rearing brood through three stages (i.e., egg, larva, and pupa), and the immature insects are oriented with their heads downward at the opening of the cells. At the end of the growth phase, each larva spins a cocoon inside the cell, resulting in a silken "cap" at the bottom.

Within both *Vespula* and *Dolichovespula* are a few species that do not establish their own nests, but whose queens invade incipient colonies of other species and eventually take over egg-laying functions. The workers of the host species then rear the new queens and males of the parasitic invaders as the latter do not produce workers. These parasitic or inquiline species present no stinging threat unless their queens are held, although the workers of the host species will defend the nests if disturbed. Thus, the parasitic species are not discussed further.

Vespula pensylvanica (de Saussure) (Fig. 2.7) and *Vespula germanica* (Fabricius), the former being native (to the western half of the United States, in spite of its name which was misspelled in the original description of the species therefore requiring

Fig. 2.7 *Vespula pensylvanica* queen.
https://upload.wikimedia.org/wikipedia/commons/4/40/Vespula_pensylvanica-Queen-1.jpg
 (Photographer Eugene Zelenko 1100 × 1100 pixels. License: GNU Free Documentation License)



perpetuation of this misspelling!) and the latter having been introduced into North America from Europe and now widespread in most of the United States and southern Canada, use sound wood for their nests resulting in a flexible gray paper nest.

The second group, usually called the *V. rufa* (Linnaeus) group because of this widespread Old World species of the group having been described first, typically develops smaller colonies built of gray paper, and the workers obtain most of their protein by predation on other insects; for these reasons the members of this group are considerably less important as stinging hazards. People who work in forests or other rural areas, particularly in cooler climates, are more likely to encounter nests made by this group. Native American members of this group include the eastern *V. vidua* (de Saussure), the western largely yellow *V. atropilosa* (Sladen), and the somewhat smaller often “polka-dotted” *V. acadica* (Sladen) typically found in cooler regions. The white-banded “black jacket” *V. consobrina* (de Saussure) and the rare northern red-spotted and white-banded *V. intermedia* (du Buysson) complete this group.

Vespula squamosa (Drury) (Fig. 2.8) and *V. sulphurea* (de Saussure) are present in the southeastern third of the United States and in California and adjacent states, respectively. They are strictly an American group having no close relatives in the Old World. The former is especially widespread and abundant, and both its aggressive defense of its colonies and its tendency to scavenge make it a risk for stinging attacks. Its colonies occasionally overwinter successfully in the southern parts of its range, thus forming huge colonies whose nests may surround a tree trunk or fill a large portion of an abandoned automobile or shed; such colonies present a severe stinging hazard to unaware passersby. Nests made by this group are typically gray, but the former may have areas of sawdust-colored paper in its nests as evidence of having “usurped” small colonies of members of the *V. vulgaris* group.

The name *Vespula* is a diminutive of *Vespa*; thus the name of the former means “little hornets” although they are not true hornets, as discussed below. The various species of *Vespula* vary somewhat in size, but in general workers range from about

Fig. 2.8 *Vespula squamosa* worker. https://upload.wikimedia.org/wikipedia/commons/2/2f/Southern_Yellowjacket_%28Vespula_squamosa%29_%287225863346%29.jpg

(Photographer: Bob Peterson 1024 × 1024 pixels. License: Creative Commons Attribution-Share Alike 2.0 Generic)



10–15 mm in length, while queens may be 20–25 mm, depending upon the species. Males are slightly longer than workers but usually not much broader.

The genus *Dolichovespula* (meaning “long [faced] little hornets”) includes a few species that are popularly called “hornets” in North America—in particular, the largest species, *D. maculata* (Linnaeus) (Fig. 2.9), is known as the bald-faced hornet. This is somewhat of a misnomer because the true hornets belong to the genus *Vespa* (of which one species is established in the United States and is discussed below). However, the bald-faced hornet is the largest native vespine in the Western Hemisphere, and its size is within the range of some of the smaller true hornets of the Old World. Its large and conspicuous gray aerial nests (Fig. 2.10) are also reminiscent of those made by some species of *Vespa*. Thus, the bald-faced hornet can be thought of as being an oversized, black-and-white aerial species of yellow jacket.

The bald-faced hornet is found throughout the continental United States, much of Canada and some regions of Alaska, but it is absent from the hot deserts and southern areas of the Great Plains. The workers and males are some 20 mm in length with the queens usually exceeding 25 mm. The lengths of individual vespine wasps and many other hymenopterans are variable because the abdomen has a series of overlapping sclerites—that is, individual sections of their chitinous shell—that “telescope,” making the length of an insect greater if well fed, full of eggs, or full of fat stored for hibernation. The bald-faced hornet has large white areas of its face, with a few white markings on the thorax and three white bands at the tip of abdomen of workers and queens, four in males. The Old World lacks a species of similar coloration, though a couple closely related species, including the widespread *D. media* (Retzius), have more typical black and yellow “yellow jacket” patterns. The bald-faced hornet is generally unaggressive unless its nest is disturbed or approached too

Fig. 2.9 *Dolichovespula maculata* worker. https://commons.wikimedia.org/wiki/Dolichovespula_maculata#/media/File:Dolichovespula_maculata_fg01.jpg (Photographer: Fritz Geller-Grimm 449 × 599 pixels. License: Creative Commons Attribution-Share Alike 2.5 Generic)



Fig. 2.10 *Dolichovespula maculata* nest. https://upload.wikimedia.org/wikipedia/commons/4/43/Bald-faced_hornet_%28Dolichovespula_maculata%29_nest.JPG (Photographer: “the High Fin Sperm Whale” 1828 × 1824 pixels. License: Creative Commons Attribution-Share Alike 3.0 Unported)



closely; even a slight disturbance will result in a mass of workers leaving the nest and attacking, often flying toward one's face.

The so-called yellow hornet, sometimes called the “aerial yellow jacket,” is another widespread member of the genus *Dolichovespula*. This species, *Dolichovespula arenaria* (Fabricius), is also found throughout much of temperate North America but is restricted to cooler climates than the bald-faced hornet; hence, it is not present in the hot deserts, much of the Great Plains, the Gulf States, or at low elevations of the southeastern United States. It looks superficially like some of the members of the genus *Vespula* discussed above, but it has the longer face typical of the genus *Dolichovespula*. There are three other (nonparasitic) species—the similar *D. norvegicoides* (Sladen) and *D. alpicola* Eck, and the white-banded *D. albida* (Sladen)—in this genus found in North America, but these are mostly restricted to northern regions and/or relatively high elevations, thus presenting less danger to human populations. Common names have been contrived for most of the social wasp as well as bumble bees, but many of them are not helpful because they are either not sufficiently descriptive or are more cumbersome than the zoological names themselves, thus being superfluous for specialists and potentially ambiguous for others.

The nests of *Dolichovespula* are made from weathered, but sound, wood such as from fence posts. Consequently, these nests are typically gray in color with strong, flexible paper. Nests are similar to those of *Vespula* except that the envelope is usually thicker (e.g., sometimes over 2 in. in *D. maculata*, with a dozen or more individual sheets of paper) because the nests are usually directly exposed to the elements. Many nests exhibit a form of “scalloping” in the envelope—that is, small sheets of paper fastened on all sides except the bottom. Nests of the bald-faced hornet may reach 2 ft in length and over a foot in diameter, often containing four or five large combs and over 400 adult insects by late summer and early autumn. Nests of the yellow hornet are similar in basic structure but on a smaller scale and with a smoother envelope with minimal or no scalloping. Nests of the latter species in areas of the Pacific Northwest west of the Cascades may approach the size of large nests of *D. maculata*. Because individual insects belonging to *D. arenaria* are smaller than those of *D. maculata*, a large nest of the former is likely to have more combs and individual cells than nests of the latter. The other species of *Dolichovespula* in North America build nests similar to, but generally smaller than, the nests of the yellow hornet to which they are closely related.

The genus *Vespa* includes about two dozen species of true hornets, native only to the Old World. The natural range of one species, *Vespa crabro* Linnaeus (Fig. 2.11), is found throughout most of Europe except the coldest regions, and by 1850 it was established in the United States, expanding from its initial introduction point in the New York City area to cover roughly the eastern third of the United States. In Europe this species is simply called “the hornet” or its equivalent in the various European languages; in North America it is known as the “European hornet” though some people refer to it as the “Japanese hornet” or “giant hornet”—the former two names not technically incorrect because the natural range of the species extends across Europe and Asia to the Pacific Coast, including Japan. The color form established in the United States is the one native to continental Europe and is sometimes

Fig. 2.11 *Vespa crabro* male. https://upload.wikimedia.org/wikipedia/commons/e/eb/Hornisse_5.jpg (Photographer: Flugwapsch 62 5184 × 3456 pixels. License: Creative Commons Attribution-Share Alike 3.0 Unported)



given the subspecific name *germana*. Anaphylaxis has been reported to stings of this species [18]. Most of the other species are native to southern, southeastern, or eastern Asia, along with associated islands as far southward as New Guinea, with the range of one species (*Vespa orientalis* Linnaeus) extending to the Middle East, northern Africa, and some areas of southeastern Europe. Another species, *Vespa velutina* (Lepeletier), has been inadvertently introduced from China into France, becoming naturalized there and in neighboring countries [19].

Nests of the genus *Vespa* may be located underground, inside cavities, or built among branches of a tree or shrub, depending upon the species, with some individual species using various kinds of nesting sites. Their paper is typically of a brown or sawdust color, similar to that of the yellow jackets of the *Vespula vulgaris* group described above. Several species tending to build in cavities typically build only a rudimentary protective envelope. Although the paper produced by *Vespa* is rather brittle, the large size of the insects allows them to produce thicker sheets sufficiently sturdy even when subjected to the weather. Some species are very aggressive in defending their nests, sometimes even if approached, while a few others will even tolerate handling of an inhabited nest.

Vespa crabro resembles a gigantic yellow jacket in body shape and coloration. Workers typically reach some 30 mm in length, being roughly the same size as a queen of *D. maculata*. Queens are somewhat larger. The nest of *V. crabro* can be found in several settings—usually inside a hollow tree or space in a wall but sometimes hanging freely under eaves or at least expanding outside a closed cavity to give the appearance of a freely-hanging nest. Rarely *Vespa crabro* nests are built underground. An extensive envelope is constructed if the nest is exposed; otherwise, the envelope is rudimentary. Cells are large, reflecting the size of the insects themselves, and a nest may contain over a dozen combs, with a few hundred insects present. Although the European hornet is not very aggressive, it will defend its nest if approached too closely or disturbed. It shares a characteristic with *D. maculata* in that it will sometimes spray its venom when attacking; if the venom gets into the intruder's eyes, severe irritation results.

An updated key to the Vespinae is provided in Kimsey and Carpenter [20]. Approximate maps of the geographic distribution of most of the species and extensive biological information is provided by Akre et al. [21].

Another important subfamily of social wasps is the Polistinae, and within this subfamily are several genera, three of which are represented north of the Mexican border: *Polistes*, *Mischocyttarus*, and *Brachygastra*. In the Americas, the Polistinae reach their greatest diversity in tropical regions; this diversity can be appreciated by reviewing the volume by Richards [22]. The taxonomy of the various genera has undergone revision since publication of Richards' work [22].

The genus *Polistes* is well represented over most of the United States and extends into southern Canada. *Polistes* contains most of the so-called paper wasps commonly seen nesting under the eaves of buildings. Other species of *Polistes* occur in most warm regions of the world. Members of this genus build a "bare" nest—that is, a single comb suspended by a petiole that lacks the protective covering or envelope typical of vespine nests. Within this genus there are several subgenera, but the proper division of the genus is still unresolved [23] and beyond the scope of this chapter. Groups of species can be recognized; for example, the widespread species *P. fuscatus* (Fabricius) is found throughout at least the eastern half of the United States and adjacent Canada, and related species including the dark reddish-brown *P. metricus* Say, the yellow *aurifer* Saussure, the small variable *dorsalis* (Fabricius), and the rather large beige and light-brown *apachus* Saussure are widespread within the eastern half, western half, southern third, and the southwest, respectively. All of these species typically build symmetrical nests (assuming a lack of interfering objects) having the supporting petiole in the middle, and males are easily recognized by having yellowish faces even if the background color is dark. *Polistes fuscatus* in cooler regions often retreats rather than attacks if the nest is disturbed, whereas more southern populations and the related species are most apt to sting when disturbed, especially if the weather is warm. Other members of this group include the tannish-gold *P. flavus* Cresson of the southwest, and the two orange-red species *P. rubiginosus* Lepeletier and *carolina* (Linnaeus) of the southeast. A second group contains such species as *P. annularis* (Linnaeus), a large (occasionally exceeding 25 mm in length) dark species sometimes known as the "red wasp," and *P. exclamans* Viereck (a smaller brown- and yellow-banded wasp known in some regions as the "guinea wasp") (Fig. 2.12). These two species inhabit the southeastern third of the United State and are especially thin wasps that build lopsided nests having the petiole near the edge and the comb hanging at an angle such that the cells open somewhat laterally. The former species tends to build its nests near bodies of water, while the latter often uses human dwellings and farm buildings where its service in preying on unwanted caterpillars somewhat offsets the potential stinging hazard. In the southwestern United States are three other species: *P. canadensis* (Linnaeus), *comanchus* Saussure, and *arizonensis* Snelling, the first two resembling *annularis* (although *comanchus* is largely yellow), while the last resembles *exclamans*. An Old World species, *P. dominula* (Christ) (Fig. 2.13), became established in the northeastern United States in the early 1980s and has spread throughout much of the country; its crisp black and yellow coloration sometimes causes it to be

Fig. 2.12 *Polistes exclamans* colony. https://upload.wikimedia.org/wikipedia/commons/5/54/PolistesExclamans_3288.JPG (Photographer: Davefoc 1987 × 2001 pixels. License: Creative Commons Attribution-Share Alike 3.0 Unported)



Fig. 2.13 *Polistes dominula* on nest. https://upload.wikimedia.org/wikipedia/commons/9/97/Wasp_March_2008-3.jpg (Photographer: Alvesgaspar 2301 × 1647 pixels. License: GNU Free Documentation License)



mistaken for a yellow jacket. Its nests, which resemble those of *P. fuscatus* with slightly smaller cells, are frequently built inside structures where the somewhat defensive wasps are easily disturbed. Finally, *P. major* Beauvois, a gold-banded species and its dark variant *castaneicolor*, are found in southern Florida and Arizona, respectively, and represent an additional species group. A few other species are present in the United States but are either uncommon or similar to those already described.

Another group of paper wasps is the large genus *Mischocyttarus*, predominantly found in tropical Latin America, with two species occurring in the United States: *M. mexicanus* Saussure and *M. flavitarsis* Saussure. The former, almost entirely restricted to Florida, is a small wasp some 10 mm in length and rather resembles a tiny *Polistes exclamans* except that the first abdominal segment is elongated, as in all species of *Mischocyttarus*, causing the insects to appear more “wasp-waisted” than the species of *Polistes*. The larger *M. flavitarsis* is about twice the size of

M. mexicanus and is mainly dull yellow with dark markings varying in shade depending on the region (and is suggestive of a small *P. comanchus*!). *M. flavitarsis* has a wide distribution in the western United States. Nests are uncovered single combs, thus similar to those of *Polistes*. The insects are relatively unaggressive. In both *Polistes* and *Mischocyttarus*, the queens are only slightly larger than the workers. In some species of *Polistes*, it may be almost impossible to recognize the queen in the colony by external morphology and size.

The final genus of social wasps to be addressed—*Brachygastra*—is mainly Neotropical and has only one species extending northward into southern Texas, usually south of San Antonio, and has been recorded in Arizona. This species, *B. mellifica* Say, is often called a “honey wasp” because it produces and stores large quantities of a form of honey (something done by very few wasps) within its large round or oval grayish nests that rival those of *D. maculata* in size. However, the nest architecture is very different from that of the Vespinae and the other Polistinae found in the United States—the cells are built on the envelope itself, forming many layers within the nest, which may contain several thousand wasps. The insects themselves are slightly smaller than yellow jacket workers (i.e., typically less than 10 mm in length) and have a different shape—the abdomen in particular has the second segment enlarged and rounded, making it look relatively short, hence the name for the genus (“short gaster” with the latter referring to the visible part of the abdomen). They are mostly black with thin yellow bands on the distal half of the abdomen. *Brachygastra* are normally rather unaggressive, but if the nests are sufficiently disturbed, the wasps will attack *en masse* and sting, with the stings sometimes being left behind as is characteristic of honey bees [24].

Bees

Bees are included in several taxonomic families, but only one family (Apidae) includes the truly social species. Two genera of social bees occur in the United States and Canada: *Apis*, which includes the introduced honey bee *Apis mellifera* Linnaeus, and *Bombus* or bumble bees.

About seven species of honey bees are known (depending upon whose classification is followed, but the most conservative systems admit at least four), and all but one are native to southern, southeastern, and eastern Asia, including associated islands. *Apis mellifera* is native to Europe, Africa, and the western half of Asia but has been introduced to both North and South America, Australia, and virtually every land in which a suitable climate exists. Honey bees have been present in North America nearly four centuries, often appearing west beyond the expanding “front” of settlement by Europeans and their descendants due to swarming [25].

Apis mellifera is made up of several strains, races, and subspecies, but due to crossbreeding and movement by human populations, the phylogeny of the species has become difficult to determine. All *Apis mellifera* forms live in colonies comprised of thousands or tens of thousands of individuals and builds waxen combs suspended vertically with hexagonal cells arranged horizontally on both sides and opening in

opposite directions. These cells are used for the storage of honey and pollen and for the rearing of brood (eggs, larvae, and pupae), with one insect developing in a cell at a time. The adult population includes a laying fertile female or queen, a few hundred males or drones, and the remainder sexually underdeveloped females or workers.

Honey bees produce honey and beeswax, two items of commercial value, but their main economic value is their pollination of commercial food crops. Unlike other social hymenopterans in temperate regions beside ants, their colonies are perennial, allowing them to mobilize a large field force during any time the weather is suitable for flight.

Because of their perennial colonies, the possibility of being stung by honey bees exists virtually any time of the year, even on winter days warm enough for flight. Because of the various strains of bees, differences in condition and health of individual colonies, effects of current weather conditions, and variation in the disposition of different colonies, honey bees range from those whose nests can be approached and even manipulated with minimal defensive behavior to those that attack spontaneously if approached within several tens of feet. Most colonies fall within the middle of these extremes, being unaggressive if the hive is not disturbed and the flight path is not hindered but becoming defensive in proportion to the severity of a disturbance. (The author's own experience with backyard hives included many pleasurable hours spent sitting a couple feet away from a hive watching the activity at the entrance without protective clothing and even included grabbing drones from the entrance while barehanded.)

The danger presented by honey bees has been augmented in the southern third of the country by the presence of the Africanized or so-called "killer" bees. Experiments in Brazil were undertaken during the 1950s to produce a strain of honey bees that would thrive well under tropical conditions, and these included the introduction of bees from Africa, which were of the subspecies *Apis mellifera scutellata* Lepeletier (Fig. 2.14). These Africanized bees appear essentially identical to several of the European strains. Original hopes were that the positive attributes of this African subspecies could be kept while reducing their aggressiveness by crossing with the European strains currently being used. However, a lack of communication among individuals at the facility resulted in the African strains being allowed to escape into

Fig. 2.14 *Apis mellifera scutellata* worker. https://commons.wikimedia.org/wiki/File:Apis_mellifera_scutellata.jpg
(Photographer: Jeffrey W. Lotz, Florida Department of Agriculture and Consumer Services, Bugwood.org 3072 × 2077 pixels. License: Creative Commons Attribution-Share Alike 3.0 Unported)



the wild, with resultant spread, eventually covering a substantial area of South America and extending northward through Central America and Mexico to achieve a presence in the United States [26, 27]. Despite the bees being nearly identical to the European strains in appearance (if anything, being slightly smaller) and the quantity and potency of their venom essentially the same, two important differences make them much more dangerous—their nesting habits and their temperament. They tend to swarm frequently and build nests in or under various structures where one would not expect to find honey bees, and very little agitation (such as with one's mere presence within the vicinity of a colony) is necessary to provoke them into frenzied stinging. Southwestern states such as California and Arizona have published descriptive literature providing warnings as well as suggestions as to means of minimizing or escaping attacks, and as other states (Florida) report the occurrence of these bees, additional warnings are being published and posted on the Internet [26–28].

Honey bees have barbs on the lancets of their stings, enabling the entire apparatus to remain in the skin of the victim allowing both the injection of additional venom and the release of a chemical pheromone that attracts additional attacking bees to the victim.

Currently 46 species of bumble bees are recognized in the United States and Canada, though several of these are considered “holarctic” in that they also occur in Europe and/or northern Asia [29]. No exotic species of *Bombus* have become established in North America. Bumble bee bodies are entirely black, while their dense pelage of hairs are of various colors—usually black and yellow—but some species have shades of red, orange, or white, depending upon the species. Queens are typically 25 mm or more in length, while workers and males are about half as long; some species are larger than others. Bumble bees live in annual colonies initiated independently each spring by individual overwintered queens, each of which builds a small nest, provisions it with pollen and honey, and lays a group of eggs eventually developing into workers—that is, their colonies follow the same basic life cycle as those of the Vespinae. Successive clusters of eggs are laid as the older immatures go through the larval and pupal stages of development and finally emerge as adults. Unlike the social wasps and honey bees, bumble bees do not build combs; rather, their nests appear as an untidy cluster of yellowish-brown cocoons, some of which are open to serve as “honey pots.” The entire nest is unlikely to exceed the size of a grapefruit, and it may be built in an abandoned rodent burrow, under a clump of grass, inside a birdhouse, or even in abandoned furniture where the interior stuffing has become exposed. Populations may reach or exceed 100 individuals, depending upon the species. Bumble bees are not aggressive away from their nests, resorting to stinging only if squeezed, but defensive behavior in or near a colony varies among species, some of which are extremely persistent in attacking an intruder. Their size and strength often enable them to sting through clothing or force their way under clothing and sting the skin directly. Before flying to attack, bumble bees often vibrate their wings in a threatening manner making a warning noise, so a person may have sufficient opportunity to leave the vicinity of the nest before the bees actually appear. Observation and listening are the best means of preventing unwanted encounters caused by disturbing colonies.

Common species include *Bombus impatiens* Cresson (Fig. 2.15) and *B. bimaculatus* Cresson in the eastern half of the United States and southeastern Canada, with *B. ternarius* Say (Fig. 2.16) in the northern part of this region, *B. bifarius* Cresson, *huntii* Greene, and *morrisoni* Cresson in the Rocky Mountain region and southwest, and *B. vosnesenskii* Radoszkowski (Fig. 2.17) and *B. melanopygus* Nylander (the dark *edwardsii* form) along the Pacific Coast. Another species widespread in the east but extending across the United States toward the Pacific Northwest is *Bombus griseocollis* (DeGeer). The number of species just mentioned should be much greater, but due to one or more factors (particularly the possible introduction of pathogens from other continents), a number of previously abundant and widespread species of *Bombus* have become rare with a couple being considered in danger of extinction. This has implications for the pollination and, hence, survival of various species of plants [29]. Queen bumble bees are less likely to attack than workers, but they are larger and possess longer stings and bigger venom sacs and thus are capable of inflicting more pain.

Several families of solitary bees have females capable of stinging if confined or squeezed against the skin. Two of these are of note—one due to its tendency to sting

Fig. 2.15 *Bombus impatiens* queen. https://upload.wikimedia.org/wikipedia/commons/e/e9/B_impatiens_queen.jpg (Photographer: Ilorban 3008 × 2000 pixels. License: Creative Commons Attribution-Share Alike 3.0 Unported)



Fig. 2.16 *Bombus ternarius* worker. https://commons.wikimedia.org/wiki/File:Bombus_ternarius.jpg (Photographer: Beatriz Moisset 550 × 452 pixels. License: Creative Commons Attribution-Share Alike 2.5 Generic)



Fig. 2.17 *Bombus vosnesenskii* worker.
https://upload.wikimedia.org/wikipedia/commons/2/21/Bombus_vosnesenskii.jpg
(Photographer: Kevin Cole
4200 × 2874 pixels.
License: Creative Commons Attribution-Share Alike 2.0 Generic)

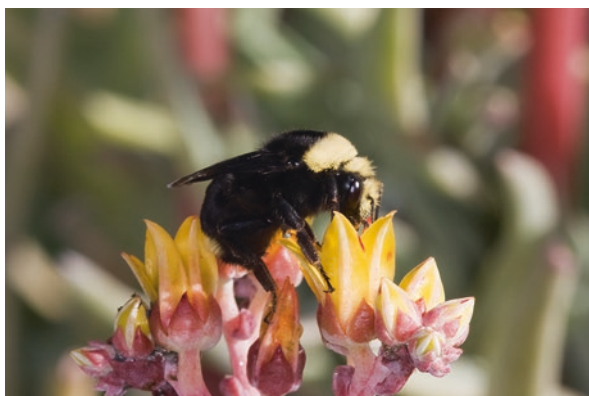


Fig. 2.18 *Xylocopa virginica* (carpenter bee) female. [https://upload.wikimedia.org/wikipedia/commons/7/7e/Xylocopa_virginica-Eastern_carpenter_bee_\(DSC_0505cr\).JPG](https://upload.wikimedia.org/wikipedia/commons/7/7e/Xylocopa_virginica-Eastern_carpenter_bee_(DSC_0505cr).JPG)
(Photographer: ysmad.com
4430 × 3730 pixels.
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and the other because of its conspicuousness. The sweat bees (genera *Halictus* and *Lasioglossum* [30] and perhaps other genera in the family Halictidae) are small, typically about 5 mm in length, and some species have developed a form of sociality. Although the insects are unaggressive and have mild stings, their tendency to land on human skin to lap perspiration causes them to be squeezed inadvertently, resulting in defensive stings.

The other notable genus of bees is *Xylocopa* which is comprised of the large carpenter bees (now in family Apidae, subfamily Xylocopinae [31]; these bees used to be placed within the family Anthophoridae with the digger bees). These large bees superficially resemble queen bumble bees but have large heads and shiny abdomens due to having less hair (Fig. 2.18). Although they are somewhat gregarious, their life cycle is solitary with no worker or queen castes among the females. They are capable of stinging, but despite their large size and presence around buildings, causing them sometimes to be perceived as threatening, they are unaggressive.

Preventing Stings

A number of websites (e.g., one provided by the Mayo Clinic [32]) offer suggestions regarding the prevention of stings, with some being more helpful than others. Some additional practical comments regarding the prevention of stings, gained from field experience, are in order. Many cases of stinging, particularly multiple stings, result from disturbances to colonies. Although any given species may build a nest in a wide range of settings, each species has certain “favorite” locations. For example, several species of *Vespula*, particularly those in the *V. vulgaris* group, are commonly found along road and stream banks where the sloping soil often provides exposed roots, crevices between layers of rocks, soil slumps, and animal burrows, any of which can be inviting opportunities for searching yellow jacket queens, and the road or stream usually provides the insects an easy opportunity for visual discovery of such potential nesting sites. Abandoned buildings provide shelter for *Polistes*, *Vespula*, and even some *Dolichovespula* if there are broken windows, open doors, or spaces between boards, all of which can serve as entrance points. The exterior provides additional nesting sites, especially under the eaves (favored by *Polistes* and *Dolichovespula*) or openings in the outside wall that lead to cavities within the wall (favored by *Vespula*, *Vespa crabro*, and honey bees). Farms provide many nesting spaces for nearly the entire range of species present in a given area; for example, spaces between bales of hay may provide nesting site for bumble bees, intact and occupied houses may have eaves or overhangs that invite *Polistes* and *Dolichovespula*, and the landscaping may provide nesting sites for *Vespula*. In addition, the branches of essentially any tree or shrub can support a colony of *Dolichovespula*, and hollow trees can harbor honey bees or European hornets. If a colony of feral honey bees is discovered, the possibility of its being of the Africanized strain should be considered if one is in the southern and southwestern areas of the United States, so it is best to avoid approaching it. Therefore, one should always take into account the possibility of a nest being nearly anywhere, with special attention to the situations described above. Any small space may serve as a nesting site for a colony of *Polistes*, and because of the small colonies produced by this genus (compared to vespines), there probably will not be enough activity to announce the presence of a colony. The author once got stung when opening the lid to the gas filler cap in a car that hadn’t been driven for a few summer months—a nest of *Polistes fuscatus* had been built near the cap during that time!

Although one is unlikely to squeeze a stinging insect purposely (except for small children who are naive as to the consequences!), situations occur in which one may inadvertently do so. For example, food or drink eaten outdoors may be attractive to yellow jackets, and even honey bees will seek sweet drinks, particularly on warm days late in the season when sources of nectar become scarce. One can get stung on the hand by squeezing the insect when picking up the cup or food item or stung in or on the mouth when eating or drinking is attempted. Lawns and fields, especially those supporting flowers, can present a hazard to anyone walking through them with floppy clothes capable of trapping insects underneath. If a bee becomes trapped

inside a trouser leg, pinching off a section of the fabric to isolate the bee away from the skin and then squeezing this section at each end a short distance from the bee will kill it such that it can drop harmlessly to the ground—a procedure successfully undertaken by the author against an unfortunate bumble bee.

As was mentioned above, avoidance of stings from imported fire ants is quite easy in most, if not all, situations, mainly by being careful not to disturb their mounds. Large colonies are easy to recognize, but small ones are less so; thus, when in fire ant country, any loose sand that appears different from the “background” soil should be suspected of hosting fire ants. However, small children, certain disabled people, and pets are at risk of disturbing fire ant mounds, so supervision by a responsible adult is necessary. In addition, the occasional colony may become established in structures or other locations where a nest may not have an obvious mound. Colonies of harvester ants are usually easy to recognize, so they should be avoided easily. Although some species of harvester ants are unaggressive, they may climb up a person’s leg if one is standing near their nest, and pressure from clothes or inadvertent squeezing is likely to result in being stung.

Quick movements for the most part are best avoided when social bees or wasps are flying about a person, but two exceptions exist. The first is that if a single insect is threatening and one is confident in his ability to kill or at least immobilize it, then striking the culprit with a well-aimed firm object (or netting it) may prevent a sting. This action assumes one is far enough from the nest that nest mates will not become involved either due to visual or chemical cues (the latter due to pheromones, discussed below). The second is that if one is about to be attacked by numerous stinging insects, removing oneself from the immediate vicinity of the angry colony by running away will prevent most if not all stings, especially if one runs a few hundred feet preferably with some intervening vegetation causing the insects to lose sight of the runner [33].

Some members of the genus *Vespula* are scavengers, and workers of these species often approach people in search of food. A yellow jacket’s back-and-forth movements about one’s hands, when one is not near a nest, are simply part of its investigating a potential food source, particularly if one has been handling any item that attracts its interest. For example, workers of *V. maculifrons* have been observed landing on a hand after a meal including shrimp had been eaten, and the wasps even bit (i.e., engaged their mandibles) in an apparent attempt to remove the skin from the hand but soon lost interest and left. If wasps are persistent, it is best to move away slowly and enter a vehicle or building if possible.

Stinging insects, in particular social species, release alarm pheromones—chemicals whose purpose is to alert their nest mates to the presence of an intruder perceived as a threat to their colony. The particular compounds released vary considerably among the species, and some are easily detected by the human nose. For example, the alarm pheromone of the European honey bee is usually described as having an odor like banana oil, while that of the yellow jacket *Vespula squamosa* of the southeastern United States reminds one of brown sugar or dried coffee. Most other alarm pheromones have more subtle odors (at least to the human nose), but their release upon stinging increases the likelihood of additional stinging, particularly

in the vicinity of the nest, communicating “I’ve just marked the enemy—let’s all charge!” Therefore, one should attempt to put distance between the nest and himself after having disturbed it, especially if a sting has already been received.

Finally, one who is hypersensitive to stings should not attempt to exterminate or remove nests but leave this task to others, including professional exterminators if necessary. In the author’s experience, a nest that has been damaged due to an unsuccessful attempt at extermination is likely to be more defensive than one that has been left undisturbed.

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