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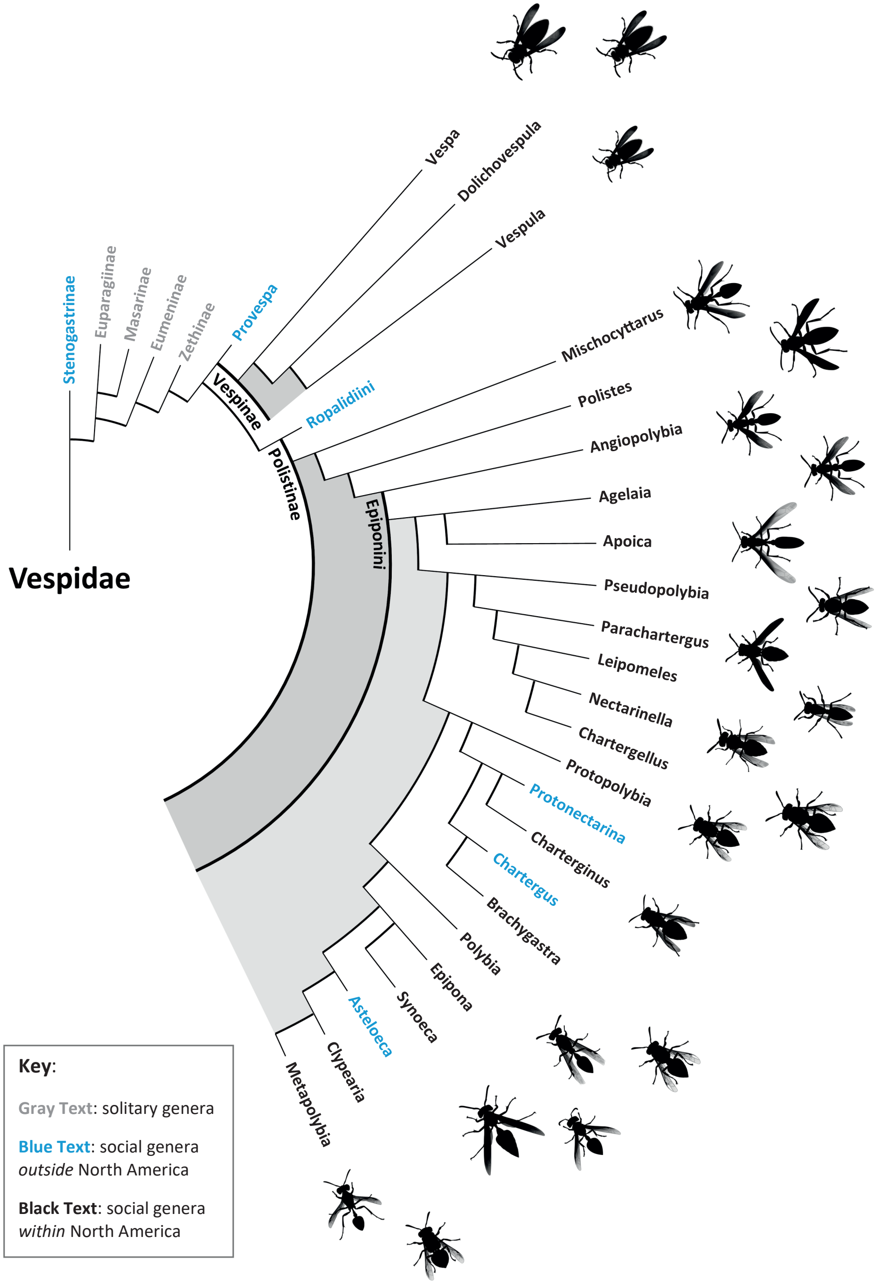
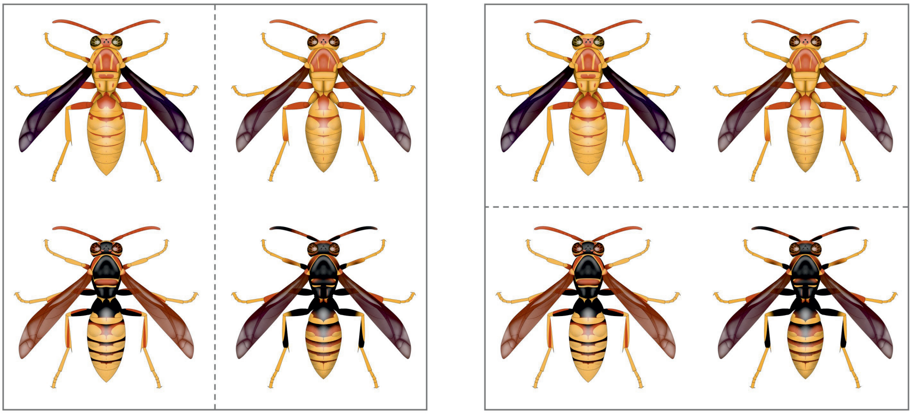


Pictured: A phylogenetic tree of social wasps in the family Vespidae based on the work of Noll F.B. et al. (2020), Hines H.M. et al. (2007), and Luo L. et al. (2022).

What Is a Species?

Taxonomy is the scientific study of how different groups of organisms are related to one another. Since so many species of wasps closely mimic other wasps, the relationships between them are very perplexing. As it turns out, wasps don't care very much about whether humans can identify them. So how did we classify these species in the first place?

Why are species grouped like this... **...and not like this?**



Pictured: Southwestern color forms of *Polistes aurifer* (pgs. 111 and 119) and *Polistes dorsalis californicus* (pgs. 140 and 142).

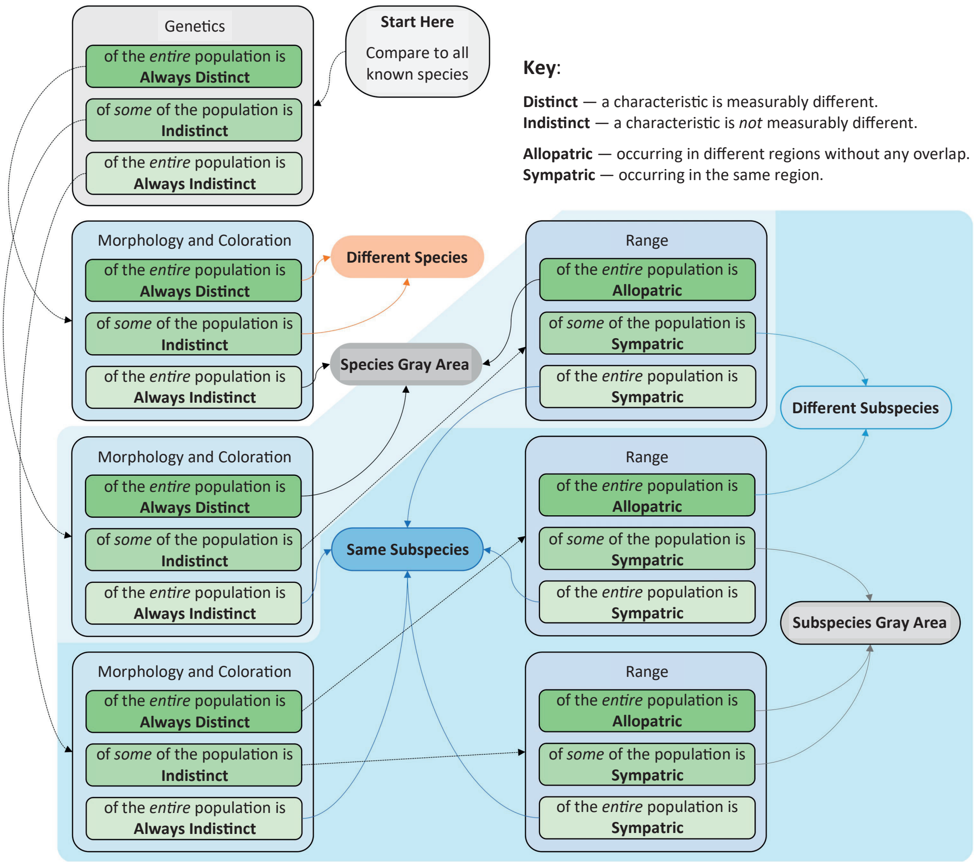
To understand what a species is, we first need to know what it isn't. We can compare any species to all other known species to see how it is similar and how it differs. Taxonomists use characteristics like a wasp's size, morphology (body shape), coloration, flight season, and DNA to describe and differentiate species. However, we can't possibly track, autopsy, and sequence the genome of every single wasp—there are simply too many. But that doesn't mean wasp taxonomy is impossible. Far from it! We just need to be clever about how we collect data.

Taxonomy is all about statistics. Rather than studying the whole, we need to study a sample of a wasp population and compare it to samples of other known species. The more samples we have, the more confident we can be about our conclusions. We'll never have a perfect picture, but we can get close.

The flowchart on the next page shows the process that is used for most modern wasp taxonomy. It is not a perfect process (and it's not the process used by all taxonomists), but it is the logic used in most recent papers about wasps.

If you follow the logic through the flowchart, you will notice that genetics play the largest roles in separating species. However, genetics are usually not enough on their own. After all, the function of genes in an organism is to encode traits that help it survive in its environment. It is important to carefully examine all aspects of a wasp population before jumping to conclusions.

Many taxonomists prefer to use the concept of a **species complex** (defined as a group of closely related species that are partially isolated but frequently interbreed where they intergrade) instead of



Pictured: A flow chart to partially answer the question "What is a species?"

the concept of **subspecies**, arguing that "species" should be the most fundamental unit in taxonomy. However—at least by modern taxonomic standards (per the flowchart above)—both systems mean essentially the same thing. I currently prefer to use subspecies, because I believe a subspecies name conveys more information about taxonomic relationships to an unfamiliar reader. In contrast, there is no quick way to determine whether a species belongs to a species complex by its binomial scientific name alone. Just be aware that passionately advocating for one system over the other is the quickest way to make a group of taxonomists want to euthanize and pin you, and then euthanize and pin each other. I promise there are better forms of entertainment.

Additionally, it is important to note that individual traits may vary independently from one another over a species' range. For example, members of a single hypothetical wasp species may tend to be larger in the west, redder in the south, and have a slightly wider gaster at low elevations, though all three traits blend together where they overlap. When taxonomists compare two populations by coloration and morphology, they must be thorough and consider as many traits as possible. A single trait by itself is typically not enough to justify the description of a new wasp subspecies or species complex.

Genetic Barcoding

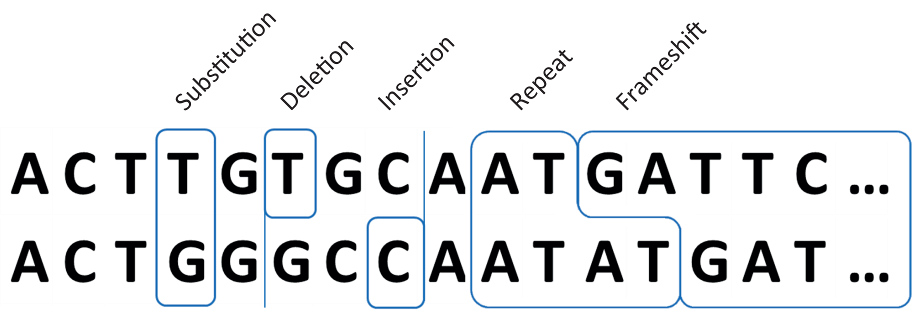
Genetic barcoding is still a very new tool in taxonomy, but it is very powerful. Below is an overview of how it works.

Every organism has a unique **genome**, which encodes the full set of instructions to create the cellular machinery it needs to survive and reproduce. A genome is composed of long strands of the molecules DNA and RNA, which are themselves composed of individual units of genetic data called **base pairs**. If we want to study the genetics of an organism, we can assemble all of the base pairs in a long sequence, and then compare many sequences together to find patterns in the noise. A wasp genome can have over 200 million base pairs, so it is very expensive and time-consuming to sequence the whole thing. Luckily, we have a shortcut.

Most of the cells in a eukaryote contain many mitochondria. Mitochondria have their own DNA because they asexually reproduce independently from the eukaryotic cells that contain them. Therefore, there are many more copies of mitochondrial DNA than eukaryotic DNA in a eukaryotic organism. If you expose a tissue sample of a eukaryote to a catalyst that duplicates DNA, the signal from the mitochondria will quickly overwhelm the sample.

In animals, all mitochondria contain a gene called "Cytochrome c oxidase subunit I" (aka COI or COX1). COX1 is several hundred base pairs long and has a very fast mutation rate. Many museums and universities have specialized equipment that can electrochemically read DNA with a special catalyst that binds to COX1. The resulting digital string of base pairs is called a **genetic barcode**.

Because COX1 mutates quickly, it can be used as a genetic clock. By counting the number of unique mutations between two organisms (and estimating the mutation rate), you can predict how long ago the two organisms shared a common ancestor.



Pictured: Common mutations in DNA (each circled in blue).

However, genetic barcoding has some important limitations. For example, DNA degrades quickly without special storage. It can be very difficult to extract usable DNA from old specimens, which means fresh specimens must be collected. Genetic barcoding is still limited to large institutions with specialized laboratories, and it's still expensive. It is often challenging for independent researchers to access this technology.

Genetic barcoding can also produce inaccurate results in certain circumstances. In animals, mitochondria are only inherited from the mother. Because of this quirk of biology, genetic barcoding can be biased by hybridization. Imagine a female wasp from species “A” mates with a male wasp from species “B” and produces fertile hybrid offspring, which eventually become a new species “C” over millions of generations. If an entomologist generates a barcode for species “C,” it will show far more genetic similarity to species “A” than species “B” because the mitochondria were inherited from the mother in species “A,” even though species “C” is equally related to species “A” and “B.” Newer techniques use both mitochondrial DNA and nuclear DNA (the DNA in the cell nucleus) to avoid this potential issue.

Genetic barcoding is a fantastic tool, but it is not a perfect method for understanding the relationships between species. Barcoding should always be done alongside traditional taxonomic research for the most accurate results.

At the time of this writing, I estimate that a quarter of all species of social wasps in North America are still unknown to science. Better access to taxonomic resources, greater community involvement, and the use of genetic barcoding will enable a more complete scientific understanding of these insects.

WASPS AND HUMANS

Let's face it, the relationship between wasps and humans is complicated. Are wasps bad for humans? Are humans bad for wasps? There is no easy answer. Wasps and humans often harm each other, but we also depend on one another. This chapter delves into those relationships to try to answer the question: How do wasps affect us, and how do we affect them?

Wasps and Industry

Social wasps interact with human industry in varied and unexpected ways. Some of these effects are outlined below, broken down by industry.

Agriculture, Forestry, and Recreation

Social wasps have a complex relationship with human agriculture. Their reputation swings wildly depending on the industry and what is being produced. For example, many orchards and meat processing plants view social wasps with absolute disdain, while many vegetable farmers view them with gratitude. So, why the difference in opinion? It all comes down to the ways social wasps can be helpful and harmful to humans.

First, the help:

Social wasps are efficient predators of many of our most destructive crop pests. They are especially effective against caterpillars including armyworms, cornworms, cutworms, hornworms, leafrollers, webworms, and cabbageworms. That makes them indispensable as a natural form of pest control for fruits and vegetables around the world. To a lesser degree, social wasps also target pest species of grasshoppers, beetles, bugs, and flies.

In North America, social wasps are important pollinators of numerous food crops such as carrots, parsnips, celery, and sunflowers as well as many spices including oregano, basil, peppermint, spearmint, lavender, fennel, dill, parsley, sage, rosemary, and thyme.

It is important to note that broad-spectrum pesticides kill beneficial insects along with pest species. Many generalized pesticides are long-lived and may persist in the environment year after year, which can wipe out beneficial predatory insects and make future pest outbreaks much worse. Generalized pesticides should be used sparingly, and only if deemed necessary as part of an integrated pest management (IPM) system. IPM is a holistic approach to reduce pests without causing unintended consequences. To learn more about IPM, refer to the EPA guidelines on IPM principles. Generalized pesticides should almost never be used in residential landscaping.

Next, the harm:

Rotting fruit is an important food source for adult social wasps (see pg. 10). This can be a big problem for fruit orchards. Aggressive wasps sometimes halt harvesting operations, costing farmers valuable time and money. Similarly, some species of social wasps are attracted to meat. Those species can be a huge headache for fishing operations and meat processing facilities.

Social wasps can also affect recreation and forestry industries by building nests in places that are inconvenient for humans (such as trees, lawns, and human structures). There is no doubt that social wasps can cause problems for us. However, those problems can usually be minimized. See pg. 2 for more information about how to avoid wasp stings.

Medicine

Wasps are medically important because of their stings. According to the Center for Disease Control (CDC), stings from bees and wasps kill about 60 people in the United States every year. Stings from honeybees and yellowjackets are most common. Most deaths occur because of an allergic reaction to the venom. The venom of different species ranges from mild to potent, but very little venom is injected with each sting. Wasp stings are designed to deter predators, so pain is much more important than lethality. Predators will remember not to mess with wasps if they've been hurt, but they will not remember if they are dead.

However, depending on the species, the venom from hundreds to thousands of wasp stings can cause tissue damage and organ failure in extreme cases. The good news is that it is very hard to accidentally get stung by thousands of wasps.

Hospitals are stocked with epinephrine and antihistamines to treat patients with allergies and rare cases of extreme stinging events. Antivenoms are typically not available for wasp stings, since wasp venoms vary between species, and death caused by wasp venom without an allergic reaction is very rare.

Wasp venom is important to medicine for another reason—and it is precisely because different species employ different toxins. Many wasps use proteins that are completely unknown to science, and they all evolved to disrupt the normal function of vertebrate tissues. That sounds like an unconditionally bad thing for humans, but it is actually fantastic! Because you know what else disrupts the normal function of vertebrate tissues? Human *medicine*. One 2016 study found a new potential antibiotic in the venom of *Polybia dimorpha* (a South American species). Another study from the same year announced the very exciting news that certain proteins in the venom of *Polybia paulista* (another South American species) destroys cancer cells without harming healthy cells. Every species of wasp creates its own cocktail of biochemicals. Studying those biochemicals (and how the wasps make them) may help us develop the next generation of human medicines.

A Very Important Disclaimer: Getting stung by lots of wasps does **NOT** cure diseases. There are many more toxins in wasp venom than there are potential medicines. Any beneficial proteins must be isolated and concentrated (and thoroughly tested) before they can be used in treatments. Novel proteins in wasp venom have a great potential for good, but we have a great deal of scientific research to do first.

Forensics

What do you do if you find a dead body in the woods? If you are a forensic investigator, you might try to catch some of the wasps nearby. Why? Wasps that scavenge for meat are picky about how long the animal has been dead. By identifying the wasps present at a crime scene, it is sometimes possible to narrow down when the victim died. This strategy is still new, and it is only possible in places that have the right kinds of wasps, since most social wasps do not scavenge for vertebrate meat (see pg. 12).

Engineering

Evolution is a learning algorithm that has been running nonstop for the past four billion years. Nowhere else will you find a better model to help solve complex problems on planet Earth. We have an unimaginable wealth of knowledge to gain by studying natural systems. In the field of engineering, the process of using inspiration from nature to create better technologies is called **biomimicry**.

A skilled engineer can glean valuable insights from any organism, but this is especially true of natural architects like social wasps. The architecture of wasp nests may lead to innovations in manufacturing, structural design, thermodynamics, and material science. The wasps themselves may inspire advances in aerodynamics, economics, nanotechnology, and learning algorithms. The inspiration is all there, waiting for the right engineer to notice it. I am proud to say that I am one of them!

While researching wasps for my first book, I noted that *Dolichovespula albida* and *D. norvegicoides* (pgs. 80 and 85) often build spherical paper nests in cavities within permafrost high above the Arctic Circle. I was amazed that these little wasps could survive in such extreme conditions.

At Owlfly, my team and I ran heat transfer experiments and learned that the nests are protected from the frost by a layer of carefully engineered air pockets within the paper structure that surrounds the nest—and the thermal properties of that structure were both highly efficient and previously unknown to science. We used biomimicry to develop a new type of insulation based on the structure of those nests, which we named YellowJacket™ after the wasps that inspired it. YellowJacket™ is American-made, lightweight, water-resistant, fire-resistant, non-toxic, non-dusting, irritant-free, and made from recycled materials. And—best of all—several of our prototypes are already ASTM certified as more energy-efficient than nearly all competing brands.

Twelve percent of all greenhouse gas emissions in the United States are attributed to heating and cooling buildings, so even small improvements in insulation efficiency can have an outsized impact on climate change mitigation. We are currently working to make even more efficient prototypes and lower costs for consumers. Our goal is to surpass the thermal resistance of every other batt insulation product on the market by the end of 2024, at a cost comparable to that of fiberglass. Wish us luck!

Entomophagy and Honey

Most human cultures—modern and historical—eat insects. Eating insects is both cheap and sustainable. They are a phenomenal source of healthy fats and proteins, they are an abundant natural resource, and many are delicious. The only thing stopping most people in the United States and Canada from eating insects is an arbitrary social understanding that bugs are creepy or gross, which is a very simplistic and outdated perspective. Many people are missing out on good cuisine.

This may come as a surprise, but lots of people eat wasps, too. In fact, according to *Edible Insects of the World* by Jun Mitsuhashi, nearly every social wasp in North America is known to be edible. This is where the distinction between “venomous” and “poisonous” is important. Wasps are venomous but not poisonous. The brood are purportedly much tastier and less crunchy than the adults (and they don’t have stingers), but you can technically eat the adults too if you’re feeling especially adventurous.

Some very important disclaimers: Please do not eat any random bug you find. Some taste bad, and some are poisonous. Always consult with an expert beforehand. No Vespid species are known to be poisonous, though not every species has been tested in a clinical setting. **DO NOT** eat wasps if you are allergic to shellfish, as most of the compounds in crustaceans are present in insects too. Attempting to harvest wasps for food without proper training is not recommended. Forage for wild food at your own risk.

If eating wasps sounds unappealing, there is always the honey! Many wasps in the tribe Epiponini produce and store honey in the same way that many bees do. Most of these wasps do not make enough honey for humans to harvest. However, the honey production of species in the genera *Brachygastra* and *Polybia* easily rival honeybees.

So why don't we see wasp honey on the shelf at the supermarket? There are a few reasons. Epiponine wasps are not domesticated like honeybees, so they are much less tolerant of human handling. Unlike the wax combs of honeybees, most wasp nests are made of paper. Wasp honey can't be harvested without breaking the entire nest open, and their honey is difficult to extract from the paper cells. Still, harvesting wasp honey can be done, and it is practiced by many indigenous American cultures.

Please be advised that the same risks for eating bee honey can also apply to wasp honey. For example, if the wasps collect most of their nectar from nightshades or rhododendrons, the honey can be toxic to humans. Attempting to harvest wasp honey without proper training is not recommended.

Pictured: Honeycombs in a nest of *Brachygastra mellifica* (pg. 330). ***Photo Credits****: iNaturalist: Jesús Moreno Navarro (jesusmoreno).*

Threats to Biodiversity

Like all life on Earth, wasps are not immune to the effects of human activity. We are in the midst of a global, human-caused mass extinction event. Modern threats to biodiversity are both severe and numerous. Still, they are not hopeless. You, dear reader, are a member of the best problem-solving species in the known universe. We can fix this if we work together. But to solve problems, we must understand them. To that end, the three greatest modern threats to biodiversity are outlined below.

Habitat Loss

Habitat loss is one of the leading causes of species extinctions in North America. Habitat is lost primarily through human activities—especially agriculture, development, and the mining and harvesting of natural resources. The extent of the damage is enormous. About 30% of temperate forests in North America have been destroyed. Less than 20% of historic prairie habitats remain. Between 1955 and 1970, the United States lost wetland habitat equivalent to about twice the land area of New Jersey, and wetlands remain one of the habitats most vulnerable to ongoing destruction.

Most natural habitat in North America was lost due to colonization and agriculture prior to the 20th century, followed by the intensive development of the 20th century. However, that doesn't mean habitat loss is no longer an issue today. Quite the contrary—the less natural habitat we have left, the more fragile our remaining ecosystems become. We must protect what remains.

Much of modern habitat damage in North America is driven by small-scale development. A wetland is drained to build housing here, a pipeline right-of-way is bulldozed through a delicate desert ecosystem there. The losses are localized, but their effects accumulate quickly. Habitat loss by itself isn't the only issue—the higher levels of pollution that frequently result from increased human activity can make habitats unsuitable for many species.

Climate Change and Range Drift

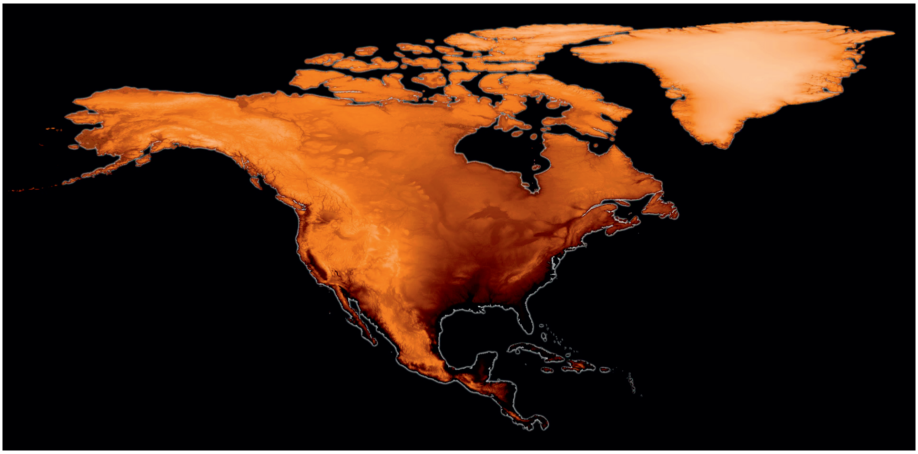
Most of the sun's energy that hits Earth is reflected back into space in the form of infrared radiation. The energy that enters and leaves Earth's atmosphere is balanced in thermal equilibrium. Or rather, it *was* balanced. Greenhouse gases (especially carbon dioxide, methane, and nitrous oxide) emitted from human activities are absorbing more and more infrared radiation and reflecting it back towards Earth's surface instead of allowing it to escape into space. As a result, the Earth's average surface temperature is now increasing exponentially—much, much faster than our ecosystems and the species they support can adapt. The global scientific community has irrefutably proven that modern climate change is real. They have also made it clear that it is an ecological and humanitarian crisis, that it is caused by human industry, and—most importantly—that we can do something about it.

The Earth is heating, but the heating itself is not our sole concern. The overall increase in atmospheric energy is causing dramatic shifts in moisture availability, air currents, ocean currents, and weather patterns. We are recording more and more severe weather events including droughts, fires, floods, and hurricanes (and we expect them to get much worse over the next century). Climate change is currently the #1 threat to biodiversity on Earth, potentially affecting all organisms (including all of the wasps in this book).

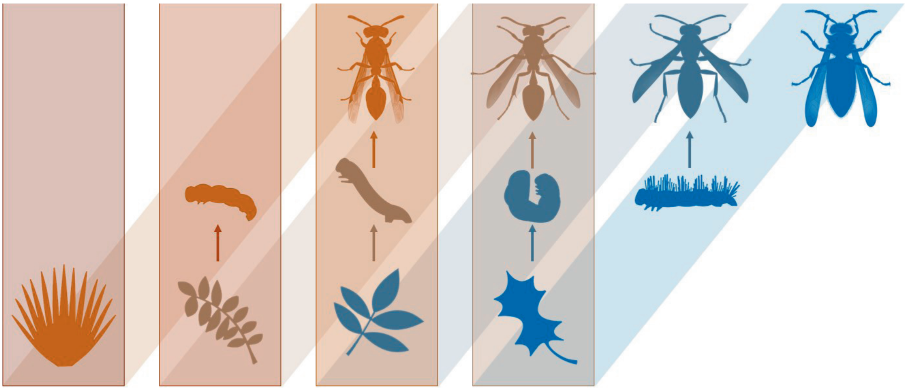
Natural disturbances have a direct effect on wildlife. Severe weather events such as fires and floods can impact huge swaths of habitat. In moderation, natural disturbances are important for many ecosystems. However, if disruptions are too frequent habitat can be damaged faster than it can recover. Over time, this can destabilize the broader ecosystem. For example, *P. d. maritimus* (pg. 117) is a subspecies of paper wasp from the island of Mangrove Cay in the Bahamas. Ninety percent of Mangrove Cay can be submerged by the storm surge of a Category 1 hurricane. The subspecies has not been recorded in the wild since 1917, which has led some scientists to wonder whether a series of severe hurricanes may have decimated their population. Coastlines and low-lying areas are also at risk from rising sea levels caused by large-scale continental ice melt in Greenland and Antarctica.

Of course, climate change has more insidious effects, too. All species on Earth have adapted to an optimal range of temperatures—a hot and cold tolerance. Because the planet is warming, the ranges of many species will shift, moving from lower elevations or latitudes (warmer climates) to higher elevations or latitudes (colder climates). We are already watching this happen as many southern species push northwards year by year across the continent. As a result, northern regions now have to contend with more pest species every year, including many species of introduced social wasps.

That being said, not all species can move. Most plants depend on specific geology, moisture, and soil conditions. Many herbivores rely on specific plants, and many predators rely on specific prey. The geology and soil aren't moving anywhere (at least, not on a comparable timescale), so even though many animals are able to move northwards, their habitats won't move with them. Range drift can cause the food web to tear itself apart. If we don't act quickly, this effect is likely to cause the extinction of many threatened species in terrestrial environments. See pg. 43 to learn more about what we can do to mitigate climate change and help reduce impacts to the most vulnerable animal and plant communities.



Pictured: The general pattern of range drift in North America, from lower latitudes and elevations (shown in darker hues) to higher latitudes and elevations (shown in lighter hues). The continent is outlined for clarity. This map is adapted from NASA elevation data in Allen J. (2005).



Pictured: The effect of range drift on the food web. Each rectangle corresponds to a latitude, and each parallelogram represents how the ranges of the species that lived there can shift. Each silhouette is symbolic of all organisms within a given niche of the food web: producers, herbivores, and carnivores.

Invasive Species

Invasive species can be incredibly harmful to ecosystems. But to understand why that is, it may be helpful to define some terms.

- **Native** – A species is considered "native" to a region if it was established in that region by natural processes without human intervention. Broadly speaking, a native species is well-adapted to survive within its local habitat, where it plays an integral role in the ecological stability and biological productivity of the region.
- **Introduced** – A species is considered "introduced" to a region if it was not established in that region prior to human activity. Species may be introduced intentionally (such as many agricultural

crops) or by accident (such as many pest insects in shipping containers). Introductions can happen due to natural events (such as organisms rafting across bodies of water on debris from large landslides), though natural introductions are extremely rare compared to human-caused introductions. In contrast to native species, introduced species have no well-established role within an ecosystem. An ecosystem is most efficient when all of its species are well-adapted to the environment and to each other. Introduced species don't fit neatly within the existing framework, so they leave gaps in the food web and reduce overall biological productivity. Humans are responsible for the introduction of tens of thousands of species beyond their native habitats, and the rate of new introductions is still increasing.

- **Adventive** – A species is considered "adventive" to a region if no stable population exists there. For example, a single individual may be disoriented by a storm and travel hundreds of miles beyond its normal range. Adventive organisms are typically unpredictable and usually have very little impact on a local ecosystem. For example, researchers found a single worker of *V. crabro* (pg. 76) in Guatemala in 2010. Guatemala has the wrong climate to support *V. crabro*, so the species could not become established.

- **Established** – A species is considered "established" in a region if a stable population exists there. Often, species are considered established if they are observed in a region for multiple successive years. An established species can be either native or introduced, naturalized or invasive.

- **Naturalized** – A species is considered "naturalized" in a region if it spreads into a new area and is able to successfully survive and reproduce to become established. A naturalized species is neither "taking over" nor "dying out," and its population is relatively stable. All introduced species can become naturalized over a sufficiently long period of time as the ecosystem adapts to their presence. However, this process may take tens of thousands of years.

- **Invasive** – A species is considered "invasive" in a region if it outcompetes other organisms in its environment and its population explodes. Invasive organisms are often described as "taking over." Most species that become invasive have been introduced, since introduced organisms usually have no natural predators or parasites in the new region. However, sometimes native species can become invasive under unstable environmental conditions, which is more likely to happen in areas with intensive human impacts.

Invasive species at any level of the food web can disrupt the whole. Invasive plants can crowd out other species and alter habitat. Invasive herbivores can decimate plant populations. Invasive predators can wipe out prey species, and invasive parasites and diseases can cause local extinctions. Any one of these can have wide-reaching effects on the entire ecosystem, often resulting in millions of dollars' worth of economic damage. Nature is deeply interconnected, and the disruptions caused by invasive species are comparable to knocking pieces out of a Jenga tower.

Several social wasps in this field guide are both introduced and invasive. The European paper wasp (*P. dominula*, pg. 109), the German yellowjacket (*V. germanica* (pg. 102), and the European hornet (*V. c. germana*, pg. 76) were all accidentally introduced from Europe and are now established as major pest species in temperate regions of North America. *Vespa mandarinia japonica* (pg. 78) was accidentally introduced to the Pacific Northwest from Japan and is responsible for the "Murder Hornet" scare of 2019. *Vespa velutina nigrithorax* (pg. 77) was just detected in the US state of Georgia in 2023 and may become similarly problematic. Invasive wasps kill native insects at alarming rates and may contribute to the decline of native butterfly populations in some areas.

A few social wasps are both introduced and native in different parts of North America. *Polistes exclamans* (pg. 178) and *P. a. apachus* (pg. 118) are native to the Great Plains. Unfortunately, they were accidentally brought to southern California by human travel, where their populations exploded. Introduced species can be especially damaging on islands. Several social wasps are invasive in the Caribbean, including *Polybia o. grenadensis* (pg. 362) in Hispaniola and *Polistes d. dorsalis* (pg. 125) in Jamaica and Hispaniola. The ecological effects of these species are not yet well-understood, but they are likely at least partially responsible for the decline of native prey species on these islands. Native yellowjackets can occasionally become invasive under the right conditions, especially due to human interference with natural systems. For example, some yellowjacket populations can boom in heavily disturbed habitats with plentiful ripe fruit or meat.

To put this into perspective, it might be helpful to note that honeybees are also an introduced species in North America. Wild honeybees may cause just as much ecological damage as invasive social wasps in certain areas because they outcompete native bees and preferentially pollinate non-native flowers. All invasive species can be damaging, and all new introductions of potentially invasive species should be avoided.

Unfortunately, it is likely that additional invasive social wasp species are coming. Mandarina-group *Vespa* (which includes the Japanese Giant Hornet) have been spotted up and down the west coast for the past 50 years in isolated sightings (accidentally released from shipping containers, etc.). So far, they have not been able to establish themselves for more than a season. But, as *V. m. japonica* proves, that may not be the case forever. North America is also at risk of long-term ecological impacts if more species of Eurasian *Polistes* and *Vespula* wasps are introduced.

How YOU Can Help

Threats to biodiversity may seem overwhelming, but luckily there are a few simple things you can do that can make a big difference. A variety of opportunities to get involved in the study and preservation of biodiversity are presented below. Some options are focused on wasps, while others address more global concerns. Pick and choose whichever activities appeal to you!

Community Science

Community science (also called citizen science) is any voluntary scientific undertaking that does not require special expertise. It is a model for science where everyone can participate—regardless of their background—and it's reshaping the boundaries of science itself. Community science has the potential to accelerate the pace of new scientific discoveries and is quickly gaining traction across almost all scientific disciplines.

There are far more organisms on Earth than there are biologists to study them. Studying ecology takes time, but we really do not have that luxury. Species are disappearing faster than we can study them. If we want to protect the environment, we need to understand it.

Community science is one part of that solution. It helps fill in the gaps (or, more realistically, *chasms*) in our scientific understanding. Community science is not a substitute for traditional science, but it is a very powerful tool. It helped make this field guide possible.

There are two main community science platforms that collect data on wasps in North America: iNaturalist.org and BugGuide.net. iNaturalist is a global database for all organisms, while BugGuide is limited in scope to arthropods in the United States and Canada. On iNaturalist, anyone can help with species identification. On BugGuide, only established experts are permitted to submit identifications. Both rely on wildlife photos submitted by volunteers, and both have pros and cons depending on how you want to use or share the data.

Note: iNaturalist is a partnership between different organizations in different regions. The organizations in North America are listed below. For simplicity, all photos in this book that were sourced through subsidiaries of iNaturalist are cited as "iNaturalist" along with the photographer's information.

Site Name	Region	Affiliated Organization(s)
iNaturalist Canada	Canada	Canadian Wildlife Federation, Parks Canada, NatureServe Canada, and the Royal Ontario Museum
NaturaLista	Mexico	CONABIO
iNaturalistGT	Guatemala	CONAP
NaturaListaCR	Costa Rica	CONAGEBIO
iNaturalistPa	Panama	MiAmbiente

So, how can you get involved? It is as simple as creating an account on your favorite community science database, taking some photos of wildlife with your camera (or your phone), and uploading your photos. Or you can use field guides (such as this one) to help make species identifications for others. You can choose the platform that works best for you or participate in both. It's that easy!

Community science helps you learn by doing while making valuable contributions to science. In the natural sciences, community science can help identify introduced species before they can become established, document rare species, and expand our knowledge of ranges, habitats, behaviors, life cycles, food webs, and color variation.

Not all community science relies on online databases. You can also volunteer with local parks, organizations, or museums to carry out more targeted research (for example, participating in field inventories or collecting specimens). It all depends on the level of involvement you prefer. There's always plenty of work to do!

Habitat Restoration

The best way to combat habitat loss is to prevent it from happening in the first place. But if that is not an option, habitat restoration—though much more difficult—is the next best thing. Habitat restoration is the process of rebuilding and maintaining native habitat. It is something that can be done on a large scale or in your own backyard.

Turfgrass lawns are one of the worst things that ever happened to native habitat in North America. They are water- and resource-intensive and they contribute little to the local ecosystem. Think of all the lawns in your neighborhood and think about how much space they take up. All that space was previously natural habitat supporting a diverse array of plant and animal species. So, what can you do about it?

Plants are the foundation of terrestrial ecosystems. One of the best ways to restore natural habitat is to plant native species and remove non-native, invasive ones—and that can include reducing the size of your lawn. You can learn more about the non-native invasive species in your area by contacting your local Department of Environmental Protection (or regional equivalent).

If you enjoy gardening, many plant catalogues highlight native species. Local nonprofit environmental organizations often provide useful information about native plants and suppliers. If you want to take a more laissez-faire approach, just let native shrubs and saplings grow naturally around the edges of your property. They are attractive and they provide a critical food source for native wildlife.

Rotting logs and fallen leaves create microhabitats for thousands of species of fungi and arthropods, and foster soil health that is critical to the survival of hibernating wasps. As dead plant matter decomposes, it provides nutrients for new plants. Where possible, you should let leaves and logs remain on the ground.

You can also volunteer at local parks and preserves to restore habitat on a larger scale. Working with others towards a shared goal of restoration can be a great opportunity to build community and meet new people. Alternatively, you can advocate for ecologically based landscaping and land-use practices within your community. Wherever you live, there is likely an organization nearby dedicated to environmental outreach or outdoor recreation. If you are reading this book, they might be a good fit for you!

Collecting Specimens

Insect collections are unbelievably valuable to science. Preserved insects can teach us so much more than photographs or written records. A clever scientist can learn everything, from the habitat to the parasites, to the life history, to even the diet of a well-preserved specimen. Large collections make the study of taxonomy and evolution possible by allowing us to compare microscopic and genetic variation across many individuals of many species in many locations at many times. Large collections also make comprehensive field guides (such as this one) possible.

The recent acceleration of human impacts on the environment makes insect collections ever more critical, as insect populations are forced to adapt or perish. For many ecosystems, the window for data collection is rapidly closing—and we need that data. In some cases, it may be our only chance to save those species from extinction.

Most large insect collections can be found in natural history museums. However, most of those museum collections consist of dozens to hundreds of smaller collections made by individual people like you. Insect collecting is a collaborative process, and you do not need to be an expert to participate. In most places, the only legal requirement to collect insects is the landowner's permission. However, the specific regulations may vary between countries and territories. Shipping preserved specimens from one country to another can be much more complicated and may require special training or governmental permissions. Consult the reference staff at your local library for more information.

There are many ways to collect live insects. You can actively catch them in a net, jar, or plastic container, or you can set out a passive trap. Wasps are most often collected at malaise traps, bait traps, and flight-intercept traps. Dead fish, rotting fruit, sugar water, or the chemical heptyl butyrate can be used as lures.

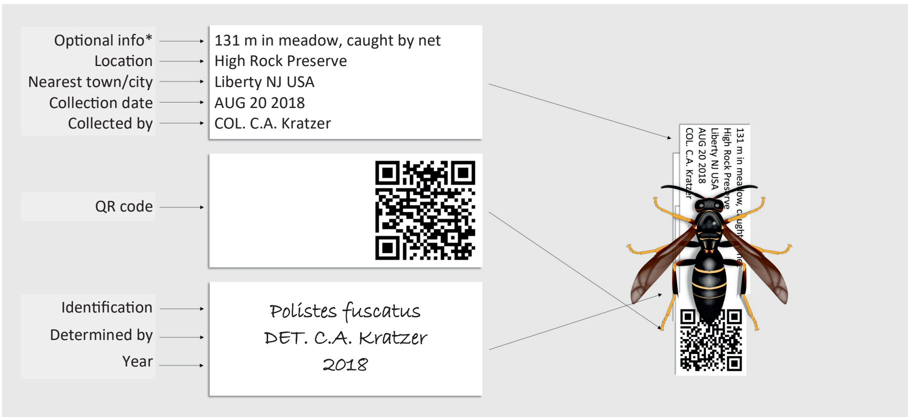
Placing an insect in a freezer will kill it. Alternatively, you can kill insects by placing a cotton ball in their container soaked in isopropyl alcohol or ethyl acetate. If you use either of these techniques, the insects will lose consciousness quickly. However, you should leave them in the container for 24 hours to make very sure they are dead.

Insect pins are much thinner and more flexible than sewing pins. You can buy packs of insect pins online. Insects can be pinned into many different materials, but plastic foam trays are used in most modern museum collections. Ideally, pinned insects should be stored in a dry, air-tight drawer or container. If the collection is too moist, it will grow mold. If it is not sealed properly, tiny dermestid beetles will find a way in (and they love to eat pinned insects). Museums typically freeze-dry new specimens at cryogenic temperatures to kill parasites and bacteria before the specimens are admitted to their collections.

Below is an example of a high-quality pinned wasp specimen. The wasp is shown in a spread position, which means its legs and wings were spread out with extra pins before the specimen was left to dry. Spreading a specimen is usually not necessary, but it can be useful to show identification characters on the abdomen and hindwings of the specimen that would otherwise be covered by the forewings. The wasp is pinned just offset from the center of the scutum. Small information cards are added to the pin afterwards.

The card on top has information about when and where the specimen was found. If you have access to a printer, you can use an online Quick Response (QR) Code generator to print a small QR Code that links to more information about the specimen (such as its database entry on a community science website), though this is optional. The bottom card shows the identification of the specimen. The bottom card is separate from the top card because it may change over time as our scientific understanding improves.

If the wasp is too small to be pinned directly, it can be attached to a card with superglue or clear nail polish, and the card can be pinned instead. Note that the colors of insect specimens fade over time, so very old specimens look much browner and duller than they did in life. Exposure to bright light can drastically accelerate the discoloration.



Pictured: How to pin a wasp. Optional info may include the coordinates, elevation, habitat, observed ecological associations, and/or capture method.

It is best to keep wasp specimens in a safe, dry, absorbent, sealed container at room temperature for at least 3 weeks after mounting before adding them to the rest of your collection. Add silicone desiccant pellets to the container (the ones that come in packaging that say "DO NOT EAT") to reduce the risk of mold.

If a dried specimen needs to be re-positioned, it can be suspended over a pot filled with steaming water on a stovetop for about 5 to 10 minutes. The steam will loosen the joints and restore some degree of flexibility until the specimen dries out again.

Some people collect wasp nests in addition to individual wasps, which is also important. However, there are some caveats. Preserving nests is more challenging than preserving individual wasps. For long-term storage, nests require larger containers and better climate controls. Collecting individual social wasps poses no danger to their natural populations. However, it is theoretically possible to over-collect the nests of some species in some locations. A wasp's nest is its home, and the wasp depends on its nest to raise its offspring. Collecting nests is also more dangerous than collecting individual wasps, simply because there are many more things that can sting you. Therefore, it is best to avoid collecting active nests of native species unless it is for a specific educational or scientific purpose. Collecting inactive nests (with permission) is a much better alternative.

If you follow these guidelines, someday you may be able to donate your collection to a museum, where it will contribute to science for generations to come.

Volunteering with Museum Collections

Collecting insects is important, but it is just as important to curate and protect existing collections. There are over 100 large insect collections in North America, and most of them are critically understaffed. Exactly why this is the case is complicated, but it frequently stems from a lack of understanding or interest within the broader community and a lack of funding for routine preservation maintenance. Even among biologists, insects are often overlooked.

There is a ton of work to be done. For example, when new collections are added to a museum, each specimen needs to be identified and added to the museum's database. This is a very labor- and time-intensive process. It is not for everyone, but if you enjoy cataloguing, the work can be rewarding.

If you want to volunteer to help curate the insect collection at your regional natural history museum, I recommend looking up its website online. If you do not know what the nearest collection is called, you can search for "[your state/territory] insect collection" or "[your state/territory] entomology museum." Once you find the website, navigate to the "contact" page and send an email to the collection manager that describes your relevant background and how you want to volunteer. There are many museums whose staff would be thrilled to have the extra help. Volunteering is also a great way to network and gain experience if you want to work in the field of entomology or museum curation.

Besides people-power, natural history museums need funding. Funding allows museums to pay for utilities and maintenance, expand collections, extend community outreach, and hire specialists and technicians. There are three loose categories of natural history collections: national collections, university collections, and private collections. National collections usually get most of their funding from the government, and university collections usually get most of their funding from their parent university. Individual donors are an important source of funding for all three. You can donate to collections yourself—and if you can, that's wonderful—but it may be even more impactful to write letters to your political representatives requesting increased funding for natural history collections. Of course, not every region in North America offers an equivalent opportunity for public support. An alternative is writing letters to museums in more affluent locales to request grant money for programs in areas with fewer resources.

It is important to remember that the some of the most unique and biodiverse regions on the continent are also among the most impoverished. Adequate funding for natural history collections in places like Central America must be given a high priority among biodiversity initiatives. Crucially, these collections must be run by locals to ensure longevity and establish a culture of reciprocity between biological research and the local community.

Investments in Sustainability

The greatest threats to biodiversity result from human industry. Therefore, mitigating the worst effects of human industry is the best way to preserve biodiversity. Enter, the diverse and innovative field of **Sustainability**. Sustainability is a framework for addressing both immediate well-being and the well-being of future generations. It seeks to meet human needs in an equitable manner while avoiding ecological damage and the depletion of natural resources.

Modern climate change is the result of accelerating greenhouse gas (GHG) emissions from human activities. We need to prioritize a massive reduction in GHG emissions. All industries and communities face unique challenges to reduce their impacts. The agricultural sector struggles with environmental issues in different ways than the transportation sector. The challenges vary by business and by region. There is no single policy or technology that can solve all environmental problems. Instead, modern climate and environmental challenges require the insight, ingenuity, and cooperation of people from all backgrounds and communities. Complex issues must be met with many creative solutions.

So what's the point? What can we do if human industry has a billion issues that harm the planet? It sounds hopeless, but it is actually a strength; there may be a billion issues, but there are also billions of us, and humans are brilliant at solving problems. Sustainability is a team project. Environmental degradation is the result of systemic problems, but systems are—by definition—created by groups of individuals. Systems can be changed. You can create meaningful progress no matter who you are or what you do.

What needs to be done the most? Fast improvements in energy efficiency, electrification, and the rapid adoption of renewable energy infrastructure (specifically solar and wind) are critical across the board. We must also invest in better freight and public transportation, as well as more effective insulation for buildings. In the United States, electricity generation from fossil fuels (coal, natural gas, and petroleum) emits about 26% of national GHG emissions. Cars and trucks together account for about 23%. Heating and cooling buildings (12%), meat and dairy production (7%), industrial chemical processes (6%), waste management (3%), and aircraft (2%) are also major contributors. Note that some of these categories overlap. Other GHG sources (including shipping, plant-based agriculture, construction, manufacturing, servers and data centers, refrigeration, etc.) individually contribute much less to the total. But taken together, these and other small GHG sources represent over a quarter of all emissions, so they are just as important to tackle.

We already have the technology to eliminate most emissions. We just need the financial investment and political willpower to make that happen. To do that, we must ensure that people working in heavily affected industries have the resources to transition to better, cleaner jobs. The way forward is difficult, but the science is clear.

It is important to note that efficient infrastructure is only as effective as it is accessible. Therefore, we also need equity. The best way to protect the environment is to empower communities to invest in sustainability and protect their own local ecosystems. We need to acknowledge that systemic inequality is a major environmental issue that harms everyone. When a community lacks the resources to stand up for itself, everyone loses. Environmental activism is not a zero-sum game. It is not "your community or mine." Equitable solutions always exist when we look for them. So we must look for them.

Educating yourself on the nuances of complicated topics and writing to your elected representatives to demand investments in sustainability can have an outsized impact on the world around you. Working together to tackle global issues that threaten biodiversity helps all species—insects and humans alike.

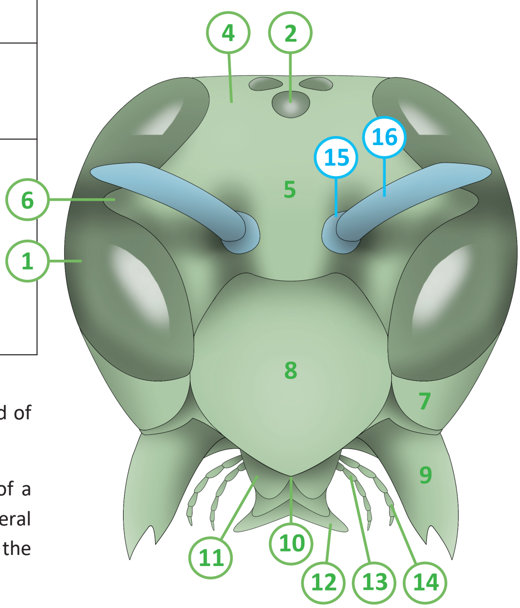
ANATOMY AND BEHAVIOR

If you want to identify a wasp you will need a basic understanding of wasp anatomy. This chapter serves as a reference for many unfamiliar terms and provides more exact language to describe the unique features of each species. It may be useful to bookmark the diagrams below when referencing the species plates in this book.

External Anatomy

	Ref.	Singular	Plural
Head	1	compound eye	compound eyes
	2	ocellus	ocelli
	3	gena	genae
	4	frons	frons
	5	corona	coronas
	6	ocular sinus	ocular sinuses
	7	ocular-malar space	ocular-malar spaces
	8	clypeus	clypei
	9	mandible	mandibles
	10	mouth	mouths
	11	maxillum	maxilla
	12	labium	labia
	13	labial palp	labial palps
	14	maxillary palp	maxillary palps
Antennae	15	antennal socket	antennal sockets
	16	scape	scapes
	17	pedicel	pedicels
	F1-N	flagellomere	flagellomeres
Throax	MES	mesosoma	mesosomata
	18	pronotum	pronota
	19	scutum	scuta
	20	tegulum	tegula
	21	scutellum	scutella
	22	metanotum	metanota
	23	propleuron	propleura
	24	mesopleuron	mesopleura
	25	metapleuron	metapleura

	Ref.	Singular	Plural
Legs	26	coxa	coxae
	27	trochanter	trochanters
	28	femur	femora
	29	tibia	tibiae
	30	metatarsus	metatarsi
	R1-N	tarsomere	tarsomeres
Abdomen	31	propodeum	propodea
	32	propodeal lamellum	propodeal lamella
	33	petiole	petioles
	GAS	gaster	gasters
	T1-N	tergum	terga
	S1-N	sternum	sterna

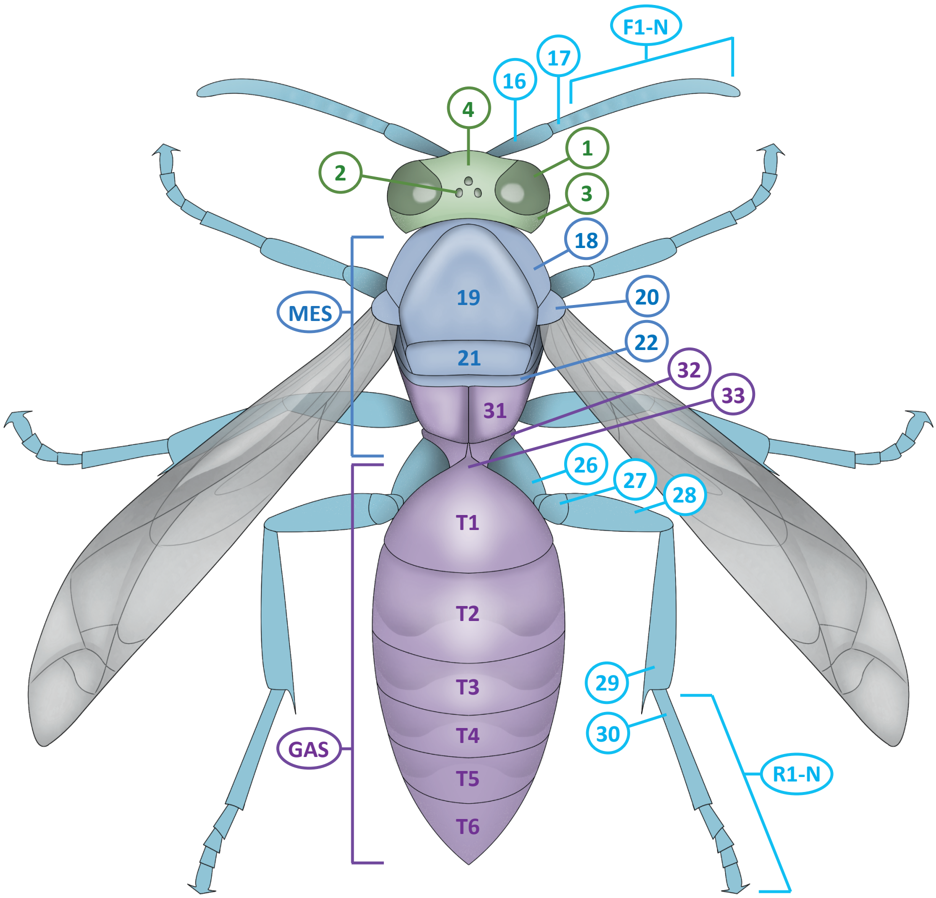


Pictured (right): An anterior view of the head of a generic wasp.

Pictured (opposite): The external anatomy of a generic wasp is shown in dorsal (top) and lateral (bottom) views. All of the colored labels in the diagrams refer to the reference table above.

Antennae

Antennae are jointed, mobile sensory organs that protrude from the front of a wasp's head. A wasp's antennae provide most of its senses of touch and smell. A single antenna is made up of four sections:


F1-N
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MES
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T1
T2
T3
T4
T5
T6
GAS
29
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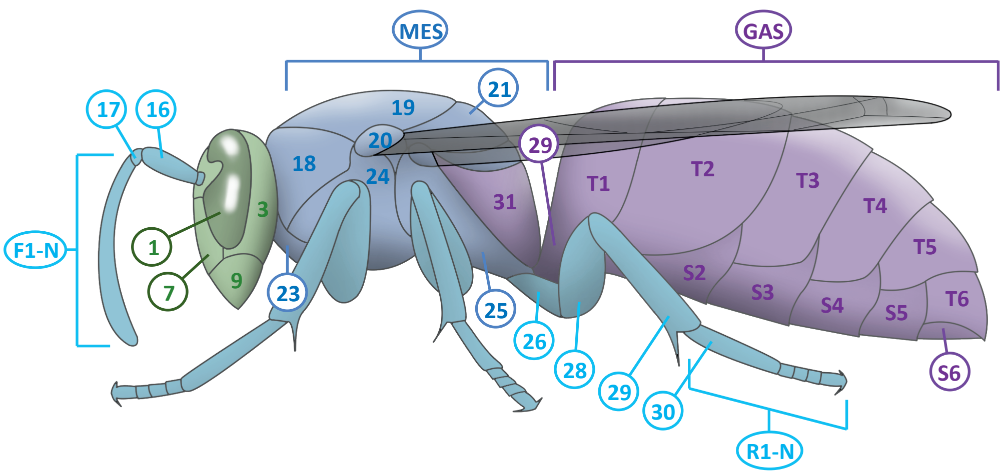
R1-N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S6
R1-N

the antennal socket, the scape, the pedicel, and the flagella. The **antennal socket** and **pedicel** are the principal joints of the antennae, each functioning similar to a human knee. The **scape** is a rigid segment that angles the flagella away from the wasp's face. The **flagella** are studded with microscopic pits and hairs that help wasps actively sense their environment. The number of **flagellomeres** (flagellum segments) varies between species. Male wasps usually have extra, longer, and/or more-flexible flagellomeres. The additional surface area helps them locate females by smell over long distances.

Head

As in humans, the head of a wasp contains its eyes and its mouth. The head is made of five main plates: the frons, clypeus, occiput, and two genae. The **occiput** (not shown) forms the back of the head above the flexible "neck" that connects the head to the thorax. The **genae** form the "cheeks" and the area behind the eyes. The lower portion of the gena (between the compound eye and the mandible) is called the **ocular-malar space**. The genae blend into the frons at the top of the head. The **frons** is the "forehead" of a wasp and can be further separated into two main regions: the ocular-sinus and the corona. The **ocular-sinus** is the space between the antennae and the compound eyes. Wasps in the family Vespidae always have a prominent ocular-sinus that partially bisects the middle of their eyes. The **corona** (or "crown") is the center of the frons between the antennal sockets and the ocelli. The **clypeus** forms the central plate of the face. The corona and clypeus are often colored in a way that helps wasps recognize each other. The clypeus also forms the top of a wasp's mouth.

A wasp's mouth is a very complicated system. It is flanked on either side by two large **mandibles**. Social wasps use their mandibles to catch and chew their prey, as well as to collect and manipulate building materials. A wasp's "tongue" is made of two main parts: the **maxillum** (the "upper tongue") and the **labium** (the "lower tongue"). Both have their own pair of "tongue fingers" called **maxillary palps** and **labial palps**, respectively. Wasps have weird tongues because of their body size. The physics of viscosity and surface tension behave differently at small scales, so wasps need complex mouthparts to eat and drink. Wasps also use their tongues to groom their legs and antennae—like strange little cats.

With the exception of *Sclerodermus* (see pg. 380), all social wasps have five eyes: two large compound eyes on either side of their heads, and three simple eyes called ocelli on top. **Compound eyes** are made up of thousands of individual lenses. The compound eyes are great for detecting movement and detail at small scales (such as a branch), but they can't see much detail at larger scales (such as a field). A wasp's compound eyes give it nearly 360-degree vision of its surroundings. Many wasps appear to have web-like patterns of color on their compound eyes. The color appears as light refracts into each lens and depends on the angle of the observer.

Ocelli are made of only one lens each. They are better at detecting large contrasts in incoming light, for example, the shadow of a bird swooping overhead. The three ocelli work together like a single larger eye. The triangular pattern helps the wasp sense where the change in light is coming from, how it is moving, and how far away it is.

In addition to the light spectrum visible to humans (from red to violet), wasps can also see in ultraviolet, which helps them to quickly locate flowers for nectar. Wasps can also sense the polarization (orientation) of light waves emitted by the sun, which acts like a built-in compass to help them navigate in open spaces. The world looks very different to a wasp.

Thorax

The thorax connects directly to the wings and the legs, which makes it the center of all locomotion. The thorax is made of six main plates: the pronotum, scutum, scutellum, metanotum, propleuron, mesopleuron, and metapleuron. The **pronotum** forms the "shoulders" of the wasp. The **scutum** (or "mesonotum") is the large central plate on the back. The **scutellum** and **metanotum** are smaller plates below the scutum. The **propleuron**, **mesopleuron**, and **metapleuron** form the "chest" on the underside of the wasp. Two pairs of wings connect to the top of the thorax through joints called **tegula**, and three pairs of legs connect to the bottom of the thorax through joints called coxae (see below).

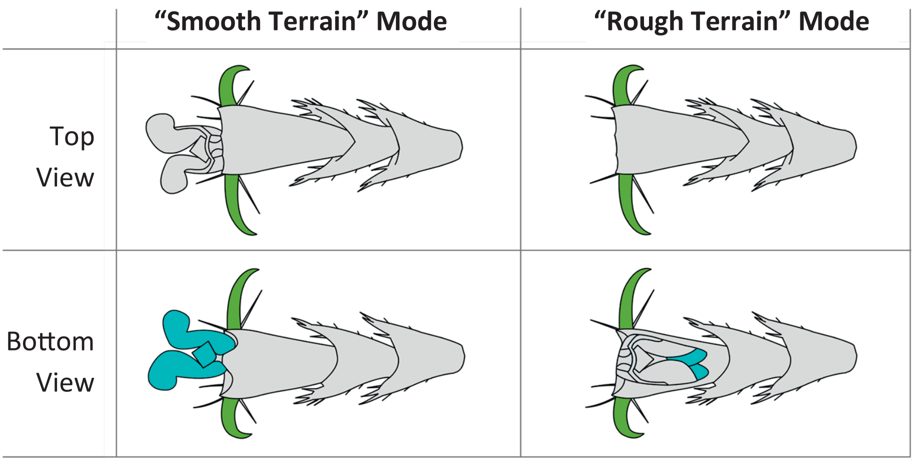
Abdomen

The abdomen is the last major body section of a wasp. It is made up of two main parts: the propodeum and the gaster. The **propodeum** looks as though it ought to be a part of the thorax, since it connects to the thorax before the "waist." But, anatomically, it belongs with the abdomen. The flared membranes at the end of the propodeum are called **lamella**. Several plates can have their own lamella, but the ones on the propodeum are the most conspicuous. The wasp "waist" is called the **petiole**. The petiole can be long or short, but it always separates the **mesosoma** (the thorax plus the propodeum) from the **gaster** (or "metasoma"). **Terga** are the interlocking plates along the top of the gaster, and **sterna** are the plates underneath. The petiole is part of the first tergum. The first sternum is usually fused with the first tergum in wasps. Female wasps always have six terga and males always have seven. A retractable **stinger** is concealed under the sixth sternum in females.

The tiny hairs on a wasp's body are called **setae**. Setae are primarily used to sense touch and vibrations, though some species also use them for display or insulation.

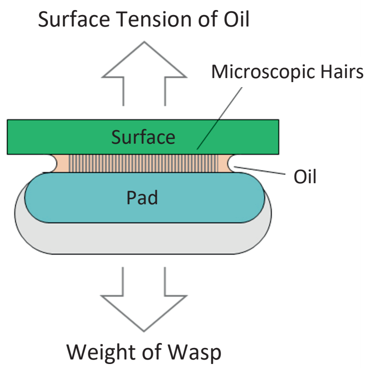
Legs

All wasps have three pairs of legs: the fore legs, mid legs, and hind legs. Wasp legs are made of four main parts: the coxa, femur, tibia, and tarsus. The **coxa** connects the leg to the bottom of the thorax. The coxa is joined to the **femur** through a joint called the **trochanter**. The femur and **tibia** are the two longest sections of the leg. The wasp's **tarsus** ("foot") is made of segments called **tarsomeres**. The first tarsomere is called the **metatarsus**, and the final segment has a little "paw" with a pair of claws and pads underneath. Wasps walk by moving their legs in an oscillating motion. First, they move the front and hind leg on one side and the mid leg on the other, and then they alternate. Wasps also use their legs to groom their body and wings.



Pictured: The two modes of wasp paws. The claws are shown in green and the pads are shown in blue.

Wasps can adjust their paws between two modes depending on the terrain. Wasps have special retractable pads that help them walk across smooth surfaces, which are withdrawn when not in use. The pads on their feet allow wasps walk upside-down with ease. How do they do it? The best current theory suggests that wasps secrete a fine layer of natural oil onto their pads and use the oil's surface tension to stick to surfaces. However, the details are still a mystery!



Pictured: The physics of wasp paws (not to scale).

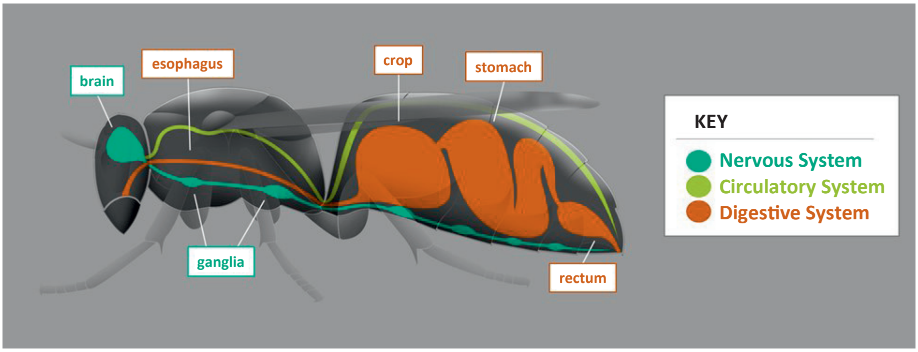
Wings

All social wasps have two pairs of wings: two front wings and two hind wings. Wasps have microscopic hooks on the leading edge of their hind wings called hamuli. **Hamuli** latch both pairs of wings together in flight and allow them to separate at rest. In the air, wasp wings function together like a single pair of large, flexible, aerodynamic surfaces. Their special wings make wasps the flying aces of the animal kingdom—right alongside agile birds and dragonflies.

Despite popular misconceptions about the physics of flight in insects, flight in wasps is well-understood by all known laws of aviation. Nevertheless, they are an aerodynamic masterpiece. Wasp wings can beat up-and-down or side-to-side depending on their movement relative to air currents, and wasps can angle their wings to maximize lift or thrust from almost any orientation. However, because their center of mass is low, wasps generally can't fly upside-down.

Most wasps fold their hind wings under their front wings when they land, which gives them better maneuverability on the ground. The hind wings are rarely seen.

Internal Anatomy



Pictured: A simplified cross-section of the nervous, circulatory, and digestive systems of a wasp.

Fat and Muscle Tissue

Wasps use a combination of muscle tissue and hydraulics to move. Wasp muscles are anchored to their exoskeleton in the same way human muscles are anchored to bones. Fat tissue is used to power the muscles. In wasps, muscle and fat tissue is concentrated in the thorax, in close proximity to the wings and legs. Strong flight muscles flex the whole thorax with every wing stroke. Most fat tissue in an adult wasp forms during its larval stage.

Respiratory and Circulatory System

Insects don't have hearts or lungs like mammals do. Actively pumping an organ would be an inefficient means of oxygen transfer at their small size. Instead, oxygen enters the body through microscopic holes in the sides of the abdomen and thorax called **spiracles**, travels along tubes called **tracheae**, and is stored in small **air sacs** distributed throughout the body. The oxygen then diffuses directly into the blood and passively travels to every cell in the body. Insect blood is called **hemolymph** and is translucent yellow-green in color. An insect's main circulatory system is a tube located on the dorsal side of the abdomen and thorax. A wasp's main circulatory system is a tube located on the dorsal side of the abdomen and thorax.

Wasps can sometimes get "out-of-breath" if they are too active. Luckily, wasps can use their whole abdomen as a giant lung. They pump their abdomen in and out to force more oxygen into their body so they can quickly react to predators or prey in their environment. Wasps can also sit in the sun to increase the rate of oxygen diffusion in their blood.

Nervous System

A human's nervous system is much more centralized than an insect's. An insect's **brain** is located within its head, and large "sub-brains" called **ganglia** can be found all along the ventral side of its body—all connected by bundles of nerves. The ganglia primarily control reflexes, but they may also contribute to decision making. That is why a dying wasp with a severed head can still sting. Humans have ganglia too, but ours are much smaller compared to the size of our brains. Wasp larvae have a very simple nervous system compared to the adults.

Despite their small size, social wasps are very intelligent animals. They are capable of advanced learning and complex social behavior. Social wasps have an impressive memory, and they can adapt their behavior based on previous experiences.

Digestive System

The digestive system of an adult wasp begins with the mouth and ends with the butt. Food enters the wasp through its mouth and moves past salivary glands, through a straw-like esophagus, then into the crop, stomach, and rectum. Adult social wasps can't eat solid food because it will not fit through their waist. The crop is especially important in social species because it functions like an internal food-safe container. Like birds, wasps can regurgitate food from their crop to feed other wasps in their nest through a "nourishing kiss" called **Trophallaxis**. Please don't try this at home.

Unlike the adults, wasp larvae can eat solid foods. The digestive system of wasp larvae consists of a mouth and a simple "pocket" where food is digested. A wasp larva only poops once. It grows a butt just before it pupates into an adult.

Reproductive System

In social wasps, both queens and workers have ovaries. However, only queens can be fertilized (see pg. 51). The males have large retractable penises that they use to mate with queens. Queens and males typically only mate once before the queen hibernates or founds a new colony. A queen has a special organ called a **spermatheca** where she can store sperm for the rest of her life.

A wasp's stinger is a modified part of the female's reproductive system, so male wasps do not have them. The stinger is retracted behind the sixth sternum when not in use. The stinger is connected to internal venom glands that replenish its toxins. Most wasps can sting many times in a row, though some tropical species (such as *Agelaia*, *Epipona*, and *Synoeca*) have robust barbs that can firmly embed the stinger after use. Like bees, these wasps often die after their sting is used, sacrificing themselves in defense of the colony.

Pictured: A pair of mating yellowjackets: the male (left) and queen (right) of *Vespula maculifrons* (pg. 99).
Photo Credits*: Author.*

Castes

In social wasps, a caste is similar to the biological sexes of other animals. Wasp castes are anatomically different from one another and have slightly different life cycles. Most social wasps have three castes: queens, workers, and males. Queens have the main reproductive role in the colony. Often, all of the other wasps in the nest are her children. However, some tropical social wasps in the tribe Epiponini have many queens in each colony. In temperate climates, queens build new colonies in the spring. Once they hatch, workers perform most of the labor. Young workers are caretakers within the safety of the nest. Older workers serve as foragers. Male wasps emerge solely to mate with new queens.

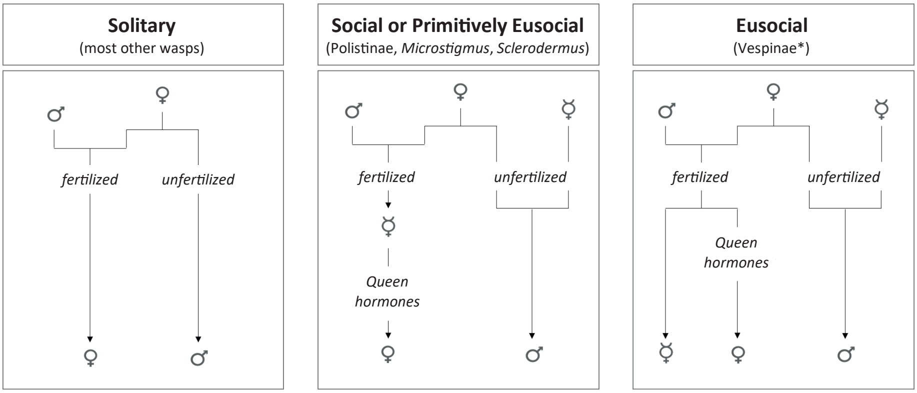
In **eusocial** species, castes are predetermined before adulthood. This decreases conflict within the colony but increases the risk of colony failure if the queen dies. The laying queen decides whether or not each larva will develop into a queen or a worker. The larva is exposed to hormones that dictate reproductive development prior to metamorphosis.

In non-eusocial species, any worker can become a queen under the right conditions. A worker can become a queen if its reproductive development is triggered by environmental or social factors (for example, if a colony's queen goes missing from the nest). The queen of a colony is determined through a social hierarchy where the most dominant wasp gets to lay the eggs.

It is important to recognize the differences between humans and wasps. Throughout history, humans have justified various social systems by drawing comparisons between men, women, and class structures to the castes of bees and wasps. However, insect castes are nothing like human genders or societies. Any direct comparison between them is not made in good faith.

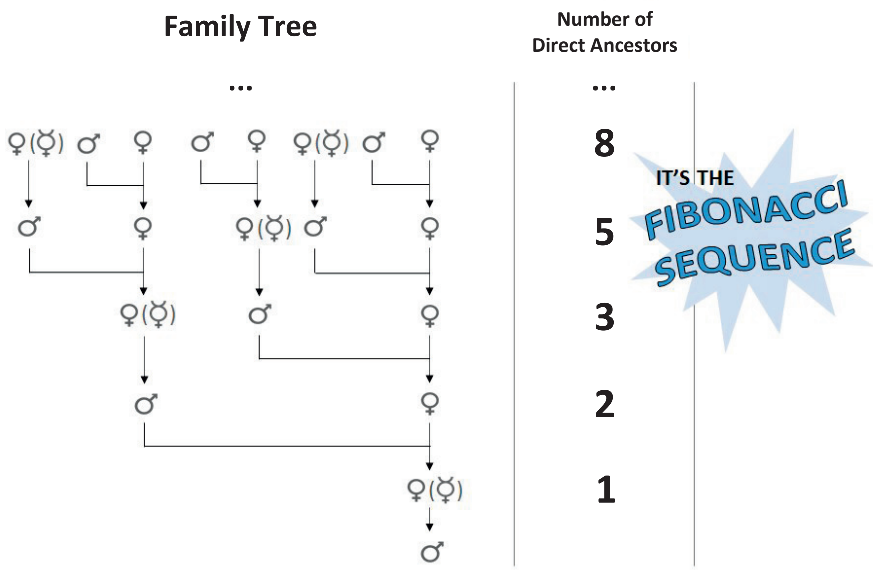
Reproduction

Reproduction in wasps is very unusual. Queens and workers have "XX" sex chromosomes, while males only have "X" (unlike "XY" in most male mammals). When an animal's embryo is fertilized, it receives one chromosome from each of its parents. That means all fertilized wasp embryos will have "XX" sex chromosomes. Here's the strange part—only unfertilized embryos can have "X" sex chromosomes. All male wasps are clones of their mothers, despite being in a different caste. All wasp eggs begin unfertilized. A queen can decide whether or not to fertilize an egg by exposing it to sperm from her spermatheca. Both workers and queens can produce males, but only queens can produce more queens and workers. How weird is that?

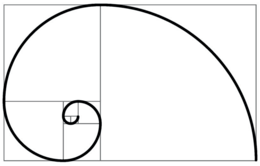


*except for obligate inquilines, whose reproduction is more like solitary wasps.

Pictured (above): Reproduction diagrams for wasps. ♀ = queens/females, ☿ = workers, and ♂ = males.
Pictured (below): How the Fibonacci Sequence appears in wasp family trees.



The peculiar mathematics of wasp reproduction results in the famous Fibonacci Sequence, where every new number is the sum of the previous two numbers. However, wasp reproduction doesn't follow the Fibonacci Sequence *exactly*. If it did, there would be more wasps than atoms on Earth 242 generations in the past. A perfect Fibonacci Sequence assumes that none of the wasps are related to any others in the same generation. In reality, many are. Crisis averted!



Nesting

Social wasps are famous for their nests. Most species make their nests out of paper, which they manufacture out of wood pulp and their own saliva. However, there are a few notable exceptions. Wasps in the subgenus *Formicicola* (pg. 332) and the genera *Synoeca* (pg. 363) and *Epipona* (pg. 361) mix mud or sand with wood pulp to form a thicker material called carton. Wasps in the genus *Microstigmus* (pg. 373) make nests out of silk and plant trichomes or sawdust. Meanwhile, *Mischocyttarus mastigophorus* (pg. 250), *Parachartergus colobopterus* (pg. 304), and wasps in the genus *Epipona* have a symbiotic relationship with special species of lichen, which they often grow on their nests as a form of living camouflage. Wasps in the genus *Sclerodermus* don't make nests at all.

Inquiline Mud Wasps: House-Flippers Extraordinaire

Mud wasps in the genus *Trypoxylon* are solitary. They usually build long nests out of mud on the sides of rocks or bridges. One tropical species, *Trypoxylon latro*, has an unusual nesting strategy. It renovates the silky nests of *Microstigmus comes* (see pg. 377) instead of building its own. Sometimes the female *Trypoxylon* even forcibly removes the current *Microstigmus* occupants to do it. Constructing mud cells inside a tiny silk nest has been likened to "building a house inside a laundry bag" (Matthews R.W. 1983). But, somehow, it works! The silk nest helps protect the *Trypoxylon* larvae from parasites and predators.

To gather wood pulp, social wasps scrape their mandibles against a source of wood. Some species target harder wood (because it has more durability), while others target rotting wood (because it is easier to collect). The wasps leave rectangular patterns of stripped wood on the surface where they're collecting fibers. Social wasps do not cause structural damage by gathering pulp.

Wasps roll their foraged materials into a ball and carry it back to their nest in their mandibles. Back at the nest, the pulp is mixed with saliva and applied to the nest. The wasp uses its mandibles to form the pulp into the correct shape and bind it to the structure. Each stripe on a wasp nest represents a single foraging trip. In this way, wasps are quite a bit like tiny 3D printers.

Adult social wasps take turns sleeping in the nest throughout the day and night, but there is always a buzz of activity. Adult wasps protect their nest from overheating by fanning their wings or by placing a drop of water at the nest entrance to evaporate. The evaporation removes heat energy from the nest, which cools it down, much like a tiny air conditioner.

Many ecologists emphasize that a colony of social insects should be regarded as a single **superorganism**. It's fascinating to think about, especially since an active nest meets most (if not all) of the criteria for life. In the wild, social wasps cannot survive without their colony, and the colony depends on the individual wasps that build it—much like the individual cells of a eukaryotic organism.

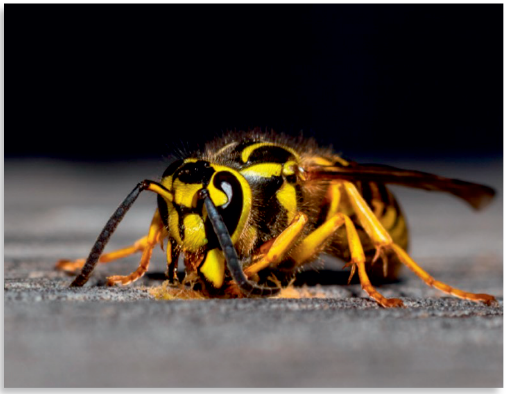
Nesting Communities: Strength in Numbers

Pictured: A nesting community of social wasps (left). If you look closely, you can spot one *Epipona* nest (E), one *Protopolybia* nest (P), and two *Mischocyttarus* nests (M). An *Azteca* ant nest (right) is built next to a *Polybia* wasp nest in the background (far right). Note the very bumpy texture of the ant nest. Most arboreal ant nests have this texture.
***Photo Credits**: iNaturalist: Cullen Hanks (cullen) and Hélio Lourencini (helio-lourencini).*

What's more intimidating to a predator than one wasp nest? Often, the answer is *many* wasp nests. Wasps often form uneasy alliances with other colonies (and even other species) to ward off common enemies. There is strength in numbers, so wasps often build nests in close proximity to one another. In exceptional circumstances, a single tree can house up to a dozen different wasp nests.

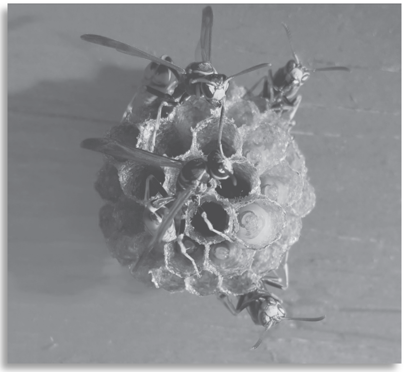
In the tropics, many social wasps prefer to nest close to arboreal ant nests. The ants are better-equipped to deter army ants, which protects the wasps; and the wasps are better-equipped to deter birds, which protects the arboreal ants. Things don't always go smoothly, though. Sometimes the wasps and arboreal ants turn on each other and fight for territorial dominance.

Some songbirds also build their nests next to wasp colonies for protection. Even the trees themselves benefit from the alliances in their branches, because the social insects aggressively protect the trees from herbivores. Some trees lure social insects to nest in them by producing nectar directly from their branches in special structures called **extrafloral nectaries**. The trees are like self-contained cities—except everyone involved is running a protection racket.



Wasps are incredibly resourceful. In rare circumstances, wasps can choose to break with tradition and use whatever resources are available in their environment to their advantage. For example, when presented with a convenient source of colored construction paper, *Polistes* wasps (pg. 109) will sometimes build rainbow nests. One colony of *Mischocyttarus flavitarsis* in Oregon even built a nest out of blue polyethylene foam scavenged from a nearby swing set. No matter the circumstances, wasps will do what it takes to protect their families.

Pictured (above): A yellowjacket gathering nesting materials (left), and a yellowjacket "printing" a new layer of material for its nest (right).
***Photo Credits**: iNaturalist: Joshua Liverman (joshl) and Shauna Moen (shaunamoen).*



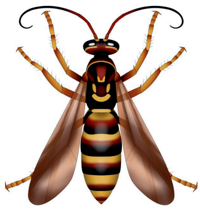
Pictured (right): A nest of *Mischocyttarus flavitarsis* (pg. 217) made from scavenged polyethylene foam.
***Photo Credits**: iNaturalist: Rose Britton (rose21).*

Mimics

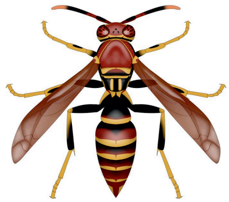
Very few predators dare to mess with wasps. Social wasps work together to defend their nests, and each wasp can sting many times. So, what do you do if you're an insect who doesn't want to be eaten? Why, you pretend to be a wasp, of course!

Visual Mimicry

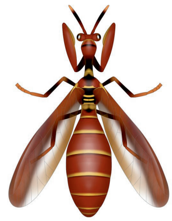
There are two main types of insects that mimic social wasps: Mullerian mimics and Batesian mimics. **Mullerian mimics** are hazardous organisms that mimic other hazardous organisms. Mullerian mimics have a strategic advantage in the wild because their predators can learn to recognize them as dangerous just by encountering other species that look similar to them. When many organisms use the same warning signals, they create a feedback loop called a **mimicry complex**. For example, many wasps in Central America have a black body with orange wings and antennae. Across the globe, most social wasps are Mullerian mimics of other social wasps, which can make identification challenging.



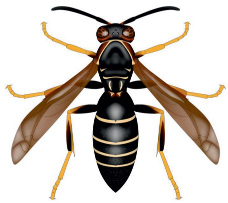
Spider Wasp
(*Poecilopompilus interruptus*)



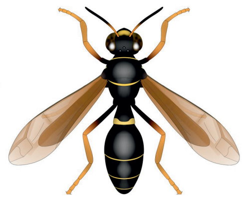
Paper Wasp
(*Polistes exclamans*, pg. 173)



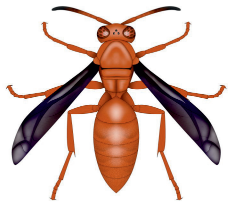
Mantidfly
(*Climaciella brunnea*)



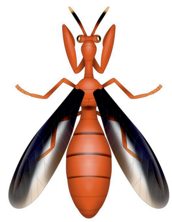
Paper Wasp
(*Polistes fuscatus*, pg. 126)



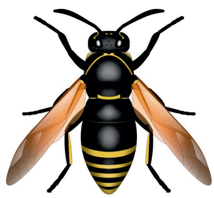
Sand Wasp
(*Saygorytes phaleratus*)



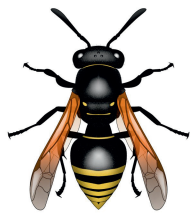
Paper Wasp
(*Polistes carolina*, pg. 139)



Mantidfly
(*Climaciella brunnea*)

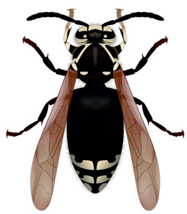


Potter Wasp
(*Pachodynerus nasidens*)

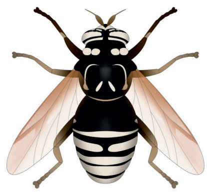


Honey Wasp
(*Brachygastra mellifera*, pg. 330)

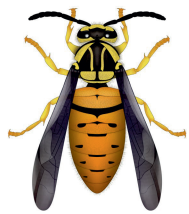
Soldier Fly
(*Hoplitimyia mutabilis*)



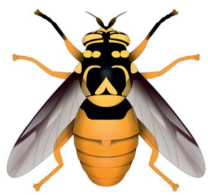
Yellowjacket
(*Dolichovespula maculata*, pg. 79)



Hover Fly
(*Spilomyia fusca*)



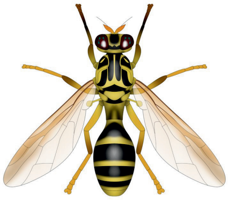
Yellowjacket
(*Vespula squamosa*, pg. 98)



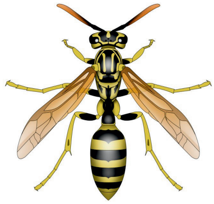
Hover Fly
(*Spilomyia texana*)

Pictured: Some of the many mimicry complexes in North America. Insects not shown to scale.

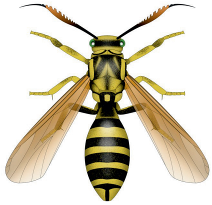
Photo References*: P. interruptus – iNaturalist: Sam Kieschnick (sambiology). C. brunnea – iNaturalist: Adriana Nelly Correa Sandoval (adriananelly), and Katja Schulz (treegrow). S. phaleratus – iNaturalist: Bernie Paquette (bepaquet). P. nasidens – iNaturalist: Rolf Lawrenz (rlawrenz). H. mutabilis – iNaturalist: Alison Northup (alisonnorthup). S. fusca – iNaturalist: (christine123). S. texana – iNaturalist: Christie (skitterbug).*



Fruit Fly
(*Anastrepha curvicauda*)

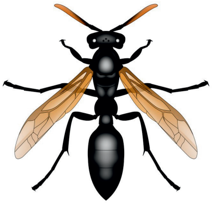


Citadel Wasp
(*Agelaia areata*, pg. 282)

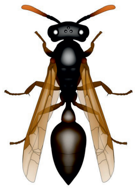


Tiger Moth
(*Pseudosphex laticincta*)

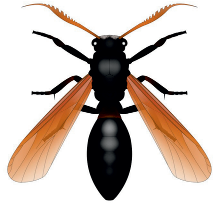
Hilted Wasp
(*Mischocyttarus carbonarius*, pg. 246)



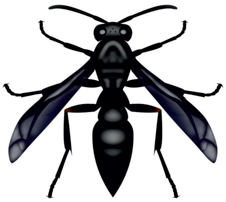
Citadel Wasp
(*Agelaia panamaensis*, pg. 290)



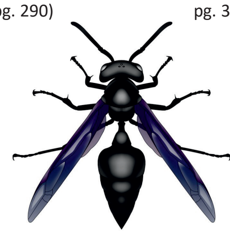
Cushion Wasp
(*Polybia lugubris*, pg. 341)



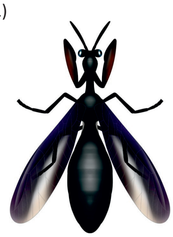
Tiger Moth
(*Pseudosphex ichneumonea*)



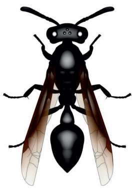
Paper Wasp
(*Polistes aterrimus*, pg. 189)



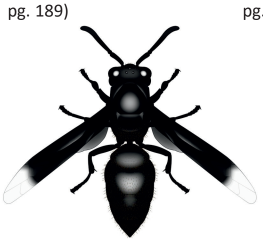
Warrior Wasp
(*Synoeca septentrionalis*, pg. 363)



Mantidfly
(*Climaciella obtusa*)



Cushion Wasp
(*Polybia tinctipennis*, pg. 338)



Guardian Wasp
(*Parachartergus apicalis*, pg. 299)

Hilted Wasp
(*Mischocyttarus deceptus*, pg. 245)

Tiger Moth
(*Pompiliodes albomarginata*)

Pictured: Some of the many mimicry complexes in North America. Insects not shown to scale.

Photo References: *A. curvicauda – iNaturalist: Juan Cruzado (juancruzado). P. laticincta – iNaturalist: Marvin Molina (tato). P. ichneumonea – iNaturalist: Karen Yukich (kyukich). C. obtusa – iNaturalist: Graham Wise (grahamwise). P. albomarginata – iNaturalist: Indiana Cristo (indianacristo).*

(continued...)

TAXONOMIC INDEX