

giant sea anemones and anemonefish is a mutualistic symbiosis which offers several benefits to each partner. There are at least three major benefits for the sea anemone: Firstly, protection — anemonefish are highly territorial and actively defend their host anemone against predators, deterring potential threats and creating a safer environment for the sea anemones.

Secondly, nutrient exchange — experiments with isotope-labelled food have shown a direct metabolic connection between anemonefish, sea anemones, and Symbiodiniaceae. Therefore, the symbiotic association contributes to the metabolism and nutrition exchange between the three partners. Interestingly, the presence of anemonefish facilitates a high symbiont density and quicker bleaching recovery in a host sea anemone.

Thirdly, oxygenation — anemonefish alleviate the hypoxic environment for sea anemones, particularly during nighttime, through an aeration-like swimming behavior. This enhanced circulation helps maintain optimal conditions for the sea anemone's physiological processes, including respiration and metabolism.

Other than providing a home, do giant sea anemones have an impact on the anemonefish? There are reports suggesting that anemonefish possibly eat giant sea anemone tentacles and/or mucus, reinforcing the complex metabolic link between partners. In addition, depending on their resident sea anemone species, anemonefish of the same species differ in color and metabolism. This serves as a nice model of environment-driven phenotypic plasticity, and it is believed that the sea anemone host impacts the neuroendocrine system of the fish, leading to pleiotropic hormonal regulations.

Does climate change affect giant sea anemone as it affects corals?

Yes, climate change profoundly impacts giant sea anemones similarly to corals. Elevated sea temperatures induce bleaching events much like in corals, by disrupting the symbiotic relationships with photosynthetic Symbiodiniaceae. During bleaching events, Symbiodiniaceae are expelled from the anemone's tissues, leading to a disruption in the anemone's

ability to obtain photosynthetically derived nutrients from the algae, which may subsequently lead to mortality. Bleaching also has a cascading effect on anemonefish living in the sea anemone, which results in stress response, a sharp decrease in fecundity, and low efficiency in recruiting fish juveniles.

Where can I find out more?

- Beldade, R., Blandin, A., O'Donnell, R., and Mills, S.C. (2017). Cascading effects of thermally-induced anemone bleaching on associated anemonefish hormonal stress response and reproduction. *Nat. Commun.* 8, 716.
- Cleveland, A., Verde, E.A., and Lee, R.W. (2011). Nutritional exchange in a tropical tripartite symbiosis: Direct evidence for the transfer of nutrients from anemonefish to host anemone and zooxanthellae. *Marine Biol.* 158, 589–602.
- Kashimoto, R., Mercader, M., Zwahlen, J., Miura, S., Tanimoto, M., Yanagi, K., Reimer, J.D., Khalturin, K., and Laudet, V. (2024). Anemonefish are better taxonomist than humans. *Curr. Biol.* 34, R175–R194.
- Litsios, G., Kostikova, A., and Salamin, N. (2014). Host specialist clownfishes are environmental niche generalists. *Proc. R. Soc. Lond. B Biol. Sci.* 281, 20133220.
- Murata, M., Miyagawa-Kohshima, K., Nakanishi, K., and Naya, Y. (1986). Characterization of compounds that induce symbiosis between sea anemone and anemone fish. *Science* 234, 585–587.
- Porat, D., and Chadwick-Furman, N.E. (2004). Effects of anemonefish on giant sea anemones: Expansion behavior, growth, and survival. *Hydrobiologia* 530, 513–520.
- Salis, P., Roux, N., Huang, D., Marcionetti, A., Mougnot, P., Reynaud, M., Salles, O., Salamin, N., Pujol, B., Parichy, D.M., Planes, S., and Laudet, V. (2021). Thyroid hormones control the formation and plasticity of white bars in clownfishes. *Proc. Natl. Acad. Sci. USA* 118, e2101634118.
- Szczebak, J.T., Henry, R.P., Al-Horani, F.A., and Chadwick, N.E. (2013). Anemonefish oxygenate their anemone hosts at night. *J. Exp. Biol.* 216, 970–976.
- Titus, B.M., Benedict, C., Laroche, R., Gusmão, L.C., Van Deusen, V., Chiodo, T., Meyer, C.P., Berumen, M.L., Bartholomew, A., Yanagi, K., et al. (2019). Phylogenetic relationships among the clownfish-hosting sea anemones. *Mol. Phylogenet. Evol.* 139, 106526.
- Verde, E., Cleveland, A., and Lee, R.W. (2015). Nutritional exchange in a tropical tripartite symbiosis II: Direct evidence for the transfer of nutrients from host anemone and zooxanthellae to anemonefish. *Marine Biol.* 162, 2409–2429.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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Primer

Parasitoid wasps

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Parasitoids — insects that parasitize other insects — have fascinating biologies that have made them darlings of the science fiction genre, owing to their wide array of innovative and often gruesome strategies for living off other organisms. These insects do not sting, but rather lay eggs on or inside their hosts, typically another insect or spider. Unlike parasites, which feed off a host without killing it, parasitoids kill their hosts — and they typically do it slowly. Parasitoids carefully keep their hosts alive for extended periods while they feed on host hemolymph and/or tissues until they are close to completing their own development. The techniques parasitoids use to feed on and manipulate their hosts are wide ranging, demonstrating multiple evolutionary pathways to achieve successful development from egg to adult.

From a human perspective, parasitoids are beneficial insects, silently controlling our garden, crop and forest pests, yet they still go unnoticed by many people. Most parasitoids are quite small, though they range in size from a fraction of a millimeter to more than fifty. The smallest insect known, about one tenth of a millimeter, is a parasitic wasp that attacks the eggs of other insects. This extremely small size has led to the evolution of a fascinating array of miniaturized features, from wings to neural cells, that have inspired design engineers. Here we focus on the largest group of parasitoids, the parasitoid wasps, and describe several features that showcase their adaptive strategies for attacking and manipulating their hosts, discuss why there are so many species, and highlight their economic importance as regulators of pest insects.

Taxonomy and diversity of parasitoid wasps

Within insects, parasitoids occur across seven different orders, including



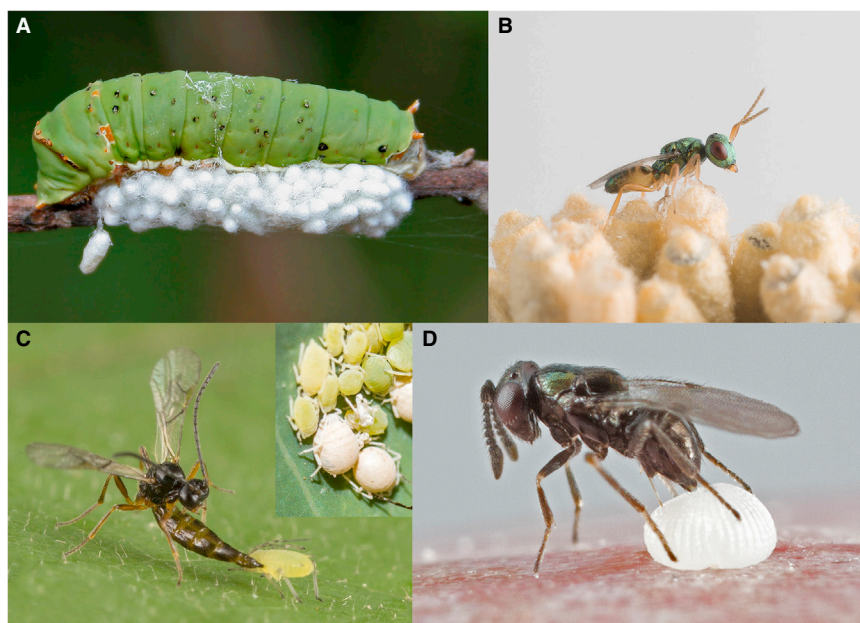


Figure 1. Parasitoid wasps lay eggs in a diversity of host species and developmental stages.

Parasitoid wasps can attack and utilize host species at various stages of host development. (A) A lime butterfly caterpillar (*Papilio demoleus*) parasitized by a koinobiont endoparasitoid wasp, *Apanteles* sp. (Braconidae, Ichneumonoidea). The caterpillar cuticle is covered with scarred wounds from exit sites of wasp larvae, which migrated into a cluster beneath the caterpillar to spin cocoons. Photo credit: © J.M.Garg/Wikimedia Commons (CC BY 3.0 DEED). (B) *Hypopteromalus* sp., a hyperparasitoid wasp (Pteromalidae, Chalcidoidea) atop cocoons of *Cotesia* sp. wasps (Braconidae, Ichneumonoidea). Photo credit: Jena Johnson. (C) *Aphidius ervi* (Braconidae, Ichneumonoidea) parasitizing a pea aphid (*Acyrtosiphon pisum*). Photo credit: Jena Johnson. (Inset) Parasitized aphids turn into ‘mummies’, in which the aphid cuticle is hardened and hollowed out by parasitic wasps to serve as a protective covering. Photo credit: © The Manic Macrographer/Flickr (CC BY 2.0 DEED). (D) A *Copidosoma floridanum* wasp (Encyrtidae, Chalcidoidea) parasitizing a cabbage looper (*Trichoplusia ni*) egg. *C. floridanum* is a polyembryonic egg–larval koinobiont endoparasitoid. Photo credit: Jena Johnson.

flies and beetles, but by far the greatest number of parasitoid species are wasps (order Hymenoptera). Ants, bees, and stinging wasps are a derived, easily recognized, and often-feared group of hymenopterans, where the ovipositor has been modified into a stinger. Although some stinging wasps are parasitoids, here we focus on parasitoid Hymenoptera that do not have a stinger, but have retained the ancestral ovipositor for laying eggs. These wasps were previously classified into an unnatural grouping called the Parasitica (to differentiate them from stinging wasps), but now are largely recognized across 12 superfamilies containing 51–59 families. The parasitoid Hymenoptera are extremely speciose, with vastly more described species than all vertebrates combined, and likely representing about 10% of all described life on the planet. Even more astounding is that many species remain undescribed because

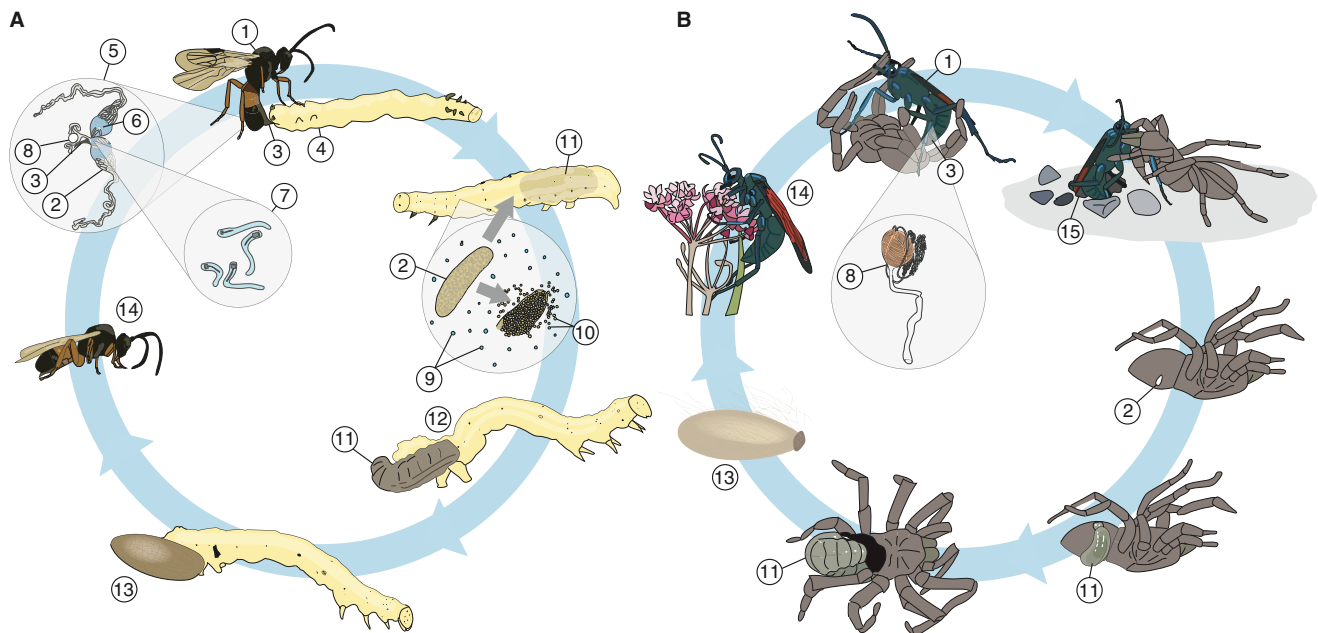
of the small and inconspicuous nature of several groups and a lack of taxonomic experts to describe new species. Conservative estimates place the number of species across the globe between 500,000 to over 1 million species of parasitoid wasps.

Hosts for parasitoid wasps are as diverse as the wasps themselves (Figure 1). Parasitoid wasps attack most orders within Insecta, but many attack other arthropods, such as spiders and ticks, and a few attack some nematodes. Any host life stage can be attacked by a parasitoid wasp: from eggs to adults, with every possible combination from egg specialists to wasps that attack larval stages and emerge from the adult stage. Most parasitoid wasps have a specific biology and are classified according to the host stage in which they lay their eggs and the stage from which they emerge as adults. Thus, a larval–pupal parasitoid wasp will lay

its eggs within the larvae of its host but complete its development in the pupal stage of its host. Parasitoid wasp growth is limited by the size of the host; thus, egg parasitoids have the smallest body size. The hosts of parasitoid wasps are found in a variety of substrates, from wood galleries, to leaf rolls, to ant nests. Whether the host is concealed within the substrate or exposed out in the open is correlated with specific morphological traits related to oviposition, such as the length, shape, and flexibility of the ovipositor. Thus, parasitoid wasp morphologies are diverse across the different lineages and are adapted to host biology and morphology. As such, there has been widespread repeated evolution of traits related to host oviposition, making parasitoid wasps a great system for studies on convergent evolution and adaptation. Until recently, convergent morphologies hindered phylogenetic reconstruction for most parasitoid wasp lineages. With simplified collection of extensive molecular data and the ability to sequence rare museum specimens for hundreds of genes, many parasitoid wasp lineages now have robust phylogenies, allowing for further studies on diversification and trait evolution. Parasitoid diversity is reflected by host and host-plant diversity, such that wasps that attack hosts that are more diverse in northern latitudes will also be more diverse in those regions. Thus, latitudinal diversity in parasitoid wasps is lineage dependent and host driven.

Life cycle and reproductive strategies

Parasitoid wasps can be specialists, focusing attacks on a single host species, or have greater host flexibility, attacking an array of related species. A few are generalists with wide host ranges, although this strategy is less common. Parasitoid wasps are either ectoparasitic, developing entirely on the outside of their host, or endoparasitic, developing within the host (Figure 2). Many endoparasitoids need to emerge from their hosts prior to pupation to complete development. Other species stay within the host to complete development and utilize the host’s exoskeleton as their pupal covering. Although less common,



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Figure 2. Parasitoid wasps employ diverse strategies for consuming hosts and overcoming host defenses.

(A) Life cycle of the koinobiont endoparasitoid *Microplitis demolitor* (Braconidae, Ichneumonoidea) and its larval caterpillar host, the soybean looper *Chrysodeixis includens*. Adult female wasps (1) deposit eggs (2) into caterpillars using their ovipositor (3) to pierce the host exoskeleton (4). *M. demolitor* ovaries (5) contain calyx cells (6) that produce bracovirus (7), giving ovaries an iridescent blue hue. A venom gland (8) produces venom, which is injected into hosts along with bracovirus and eggs. Soon after parasitism, bracovirus infects host hemocytes (9), and genes encoded on viral DNAs are used to produce virulence proteins for host manipulation. When eggs hatch, the serosal membrane underlying the egg shell dissociates to liberate teratocyte cells (10) into the host hemolymph. Wasp larvae (11) grow and undergo several cycles of molts as they feed on host hemolymph. At the final stage of larval development, wasps exit the host (12) and spin a cocoon (13) before molting to the pupal stage. After body-plan remodeling in the pupal stage, wasps molt a final time and use their mouthparts to create a hatch in their cocoon and emerge as mature adults (14). (B) *Pepsis* sp. tarantula hawk (Pompilidae) parasitizing an *Aphonopelma* sp. tarantula. *Pepsis* sp. wasps are idiobiont ectoparasitoids of a metallic blue-green color. An adult female wasp (1) stings a tarantula host, injecting venom from her venom glands (8) resulting in host paralysis. The wasp then drags the paralyzed spider into a burrow (15), where it lays an egg (2) on the abdomen of the tarantula. The egg hatches and the larva (11) begins to feed upon the host (first on hemolymph, then tissues) while growing and undergoing several cycles of molting. The larva spins a cocoon (13) and pupates within. Eventually, wasps cut open their cocoon and emerge as mature adults (14).

some female parasitoid wasps will lay eggs near hosts, and then the young mobile larvae must locate or attach to their hosts. When the female lays her eggs on or in a host, she will deliver venom proteins that either arrest development of the host permanently (idiobiosis) or allow for continued development (koinobiosis), often after a short period of temporary paralysis. Typically, koinobionts attack young larval stages of insects as further host growth benefits the parasitoid wasp as it becomes a more substantial food source. Koinobionts also tend to be endoparasitoids, and thus do not require strategies to prevent being sloughed off when the host molts to the next life stage. Idiobionts are more commonly ectoparasitoids and typically attack stages where further development is not necessary or desired, such as egg or pupal stages.

The pupal stage is typically a long and vulnerable stage for a host, creating a perfect food source for many ectoparasitoid wasps.

Most parasitoid wasps are primary parasitoids, attacking a non-parasitic host, but some are known as hyperparasitoids and use other parasitoid wasps as their hosts; this may be an optional choice (facultative) or one that is necessary for survival (obligatory). Solitary parasitoids are the most common, where a single wasp develops and emerges per host. A rare but interesting case is polyembryonic wasps, in which a single wasp egg undergoes division to form multiple clonal embryos, sometimes resulting in thousands of offspring. Polyembryonic wasps can have distinct larval morphs: 'reproductive' progeny that emerge as adults and 'soldiers' that attack other embryos or larvae. The soldier

morph prevents competitors from using the same host or removes supernumerary eggs of a single sex to manipulate the sex ratio of the brood. Other wasp species are gregarious, where one female will lay multiple eggs per host and most of the developing larvae will survive to adulthood. This greater clutch size per host may have an adaptive advantage if hosts have patchy distributions. Superparasitism is when more than one female of the same species lays eggs in a host. However, superparasitism is often not a viable strategy for survival for solitary species; thus, larvae wage war resulting in a single victor. Interestingly, this victor may have a better chance of successful parasitism due to a higher dose of host manipulation factors from multiple oviposition events (see below). Alternatively, multiple parasitism is when females of different species

lay eggs in the same host, and this results in direct competition among developing parasitoid larvae, typically with only one surviving. Competition either from hyperparasitoids or multiparasitism may have driven the evolution of wasps to attack younger host-life stages where they can hasten development before competitors arrive.

Parasitoid wasp ecology

Parasitoids have an enormous impact on ecosystems as top-down regulators of other insects. With few exceptions, it is thought that nearly every species of insect is prone to attack by at least one species of parasitoid wasp. Insect ecologists have spent decades in the field collecting parasitized host insects followed by rearing and identification of parasitoids to build food webs and collect data on survival and mortality to quantify the impact of parasitoids on herbivore populations. In one famous case study of parasitoids of leaf miners in Costa Rica, approximately a third of leaf miner mortality could be attributed to parasitoid wasps. This effective top down control has made parasitoids important tools for sustainable agriculture. Native parasitoids play an important role in non-chemical control of crop and forest pests. Parasitoids have also been imported for biological control of introduced pest species. Though often successful, some introduced parasitoids failed to establish or proved dangerous when native non-target species were parasitized along with the pest. Current approaches to biological control aim to introduce only specialist parasitoids after considerable research into host range. Much research has also gone into augmenting or protecting existing native parasitoid populations in agricultural settings to reduce the need for chemical control. Due to their importance in natural and agricultural ecosystems, parasitoids have provided inspiration and data to test numerous mathematical models predicting fluctuations in host and parasite numbers over time.

Behavioral ecology and communication

Although parasitoids exhibit behaviors that are similar to those

used by other insects (for example, courtship and mating behaviors), the parasitic lifestyle has engendered several distinctive behaviors and communication strategies. The crucial need to locate hosts involves finding the correct coarse- and fine-grained habitat via sensing of volatiles, colors, shapes, sounds, or vibrations through substrates in which hosts are concealed. Antennation (touch sensing with antennae) and detection of surface compounds such as chemical trails or pheromones are used in combination with visual, sound, touch, and/or temperature cues to find hosts within a habitat. Parasitoids can use cues from host actions such as feeding or defecating to find hosts. Plant volatiles released during damage from herbivorous insects can also be used by parasitoids to locate hosts. Herbivore saliva can even trigger the plant to release a specialized bouquet that can attract parasitoids to specifically attack those herbivores; ostensibly a 'call for help' from plant to wasp. Individual parasitoids can then learn these cues and use them to find appropriate hosts. Once identified, acceptance of a host as suitable for oviposition involves further specialized behaviors to confirm the correct identity and suitability of hosts, taking into account host developmental stage and/or size and the presence of other parasitoid progeny. Both the antennae and ovipositor insertion can be used to effectively taste the host's external and internal environment prior to acceptance. All hymenopteran parasitoids are haplodiploid (diploid females and haploid males), with rare exceptions. Females control fertilization as they can store sperm from matings, and thus, female wasps can choose to produce males by simply not fertilizing eggs as they are oviposited. There is much theoretical and empirical evidence that parasitoid females will often lay female eggs into larger hosts, presumably because female progeny benefit most from having more resources to produce eggs, while male eggs will be laid into smaller, resource-poor hosts. Some parasitoid species mark hosts with physical or chemical marks to deter further parasitization attempts by members of their own or other

species. However, these marks can then be utilized by hyperparasitoids to find their parasitoid hosts.

Parasitoid-microbe interactions

Like many insects, parasitoids are often exposed to microbes and can engage in long-term symbiotic interactions of a pathogenic, commensal, or mutualistic nature with bacteria, viruses, and other types of microbial organisms. Intracellular bacterial symbionts that manipulate reproduction are very common in parasitoids. These reproductive manipulators induce phenotypes that favor their own transmission even though in some cases the symbionts decrease wasp fitness. Several genera of bacteria are known to manipulate reproduction in parasitoids, including *Wolbachia*, *Cardinium*, *Spiroplasma*, *Arsenophonus*, and *Rickettsia*. These reproductive manipulators can each induce one of the following phenotypes: cytoplasmic incompatibility (infected males are incompatible with females that are not infected with the same symbiont type), thelytokous parthenogenesis (unfertilized eggs giving rise to daughters), and male killing (death of males during embryogenesis). Reproductive manipulators can also underlie speciation when hybrid lethality is caused by cytoplasmic incompatibility. Characterization of the molecular mechanisms underlying reproductive manipulation represents the cutting edge of this field in the last decade.

Parasitoids can have a community of bacteria living in their gut, the diversity of which is expected to differ depending upon its life history (relatively sterile internal host environments for larval endoparasitoids compared to ectoparasitoids) or life stage (larval host feeding compared to adult feeding cessation or feeding on nectar, honeydew, or host hemolymph). Gut content has only been assessed in a few species and largely found to be variable, with the only discernible pattern being repeated detection of species within the Proteobacteria and Firmicutes. For the most part, the role of gut bacterial symbionts in parasitoids is unknown, with the exception of *Nasonia* species,

in which gut bacteria have been linked with hybrid sterility and suggested as a mechanism for speciation.

Parasitoids can be infected by a diverse range of viruses as well, with accelerating discovery linked to decreased costs of sequencing. The effects of these viruses upon parasitoids is often unknown, but some are known to function as pathogens, commensals, or mutualists. Some are vertically transmitted from females via eggs, whereas others are horizontally transmitted. Hosts and parasitoids can easily share viral symbionts, which can be acquired by parasitoids from hosts via ingestion, wounding, or surface contamination. Viruses in the Filamentoviridae can manipulate parasitoid behavior to favor superparasitism, which promotes horizontal transmission of the virus, sometimes to the detriment of the wasps themselves. Another virus in the Entomopoxvirinae is a mutualist and can substantially increase the likelihood of success in parasitism. The genetic basis of viral effects upon parasitoids is often unknown and is a topic of current research.

Host manipulation strategies

Parasitoids have an arsenal of specific adaptations that enable their parasitic lifestyle. Ovipositors are extensions of abdominal segments that are used to penetrate and lay an egg within host insects, but also allow parasitoid wasps to assess potential hosts and to inject venom (and sometimes viruses). Hymenopteran parasitoids have venom glands that function to produce, store, and deliver venom. Venom constituents vary between species but can consist of proteins, biogenic amines, and other compounds. Genes encoding venom proteins are often co-opted from those involved in other physiological processes and convergence of certain types of venom proteins is common across lineages. The effects of venom upon hosts varies and can influence host behavior, immunity, development, and nutritional value. Venom can result in host paralysis (a strategy often used by idiobiont ectoparasitoids) or even change host behavior to protect or guard developing wasps when feeding or

developing externally. Koinobiont endoparasitoids inject venoms that can manipulate host immunity to prevent recognition and attack of eggs and larvae, and alter host physiology to increase availability of nutrients for wasp larvae ingestion. Venom can also prevent progression of host development (idiobiosis) to provide a consistent environment for growth of developing parasitoids.

While ovipositors and venom are ancestral characteristics of hymenopteran parasitoids, many other strategies are employed in interactions with hosts in a taxonomically limited manner. For example, teratocytes are cells that dissociate from parasitoid egg serosal membranes after hatching to circulate in hosts. Although the roles of teratocytes in hosts are often undescribed, these cells contain the full genetic coding capacity of wasp cells in a host environment and in some cases are known to secrete factors that influence host nutrient availability, immunity, or development. In other cases teratocytes are thought to absorb host nutrients and serve to feed developing wasp larvae upon their ingestion. An incredible adaptation that has recurrently evolved in parasitoids is the integration of viruses into wasp genomes. In certain lineages of parasitoids, sets of genes from large DNA viruses entered into the genome of wasp ancestors, creating heritable viruses referred to as ‘domesticated endogenous viruses’ (DEVs). These viruses, now permanently a part of the wasp, remain functional and are produced in wasp ovaries to be injected into host insects. In hosts, DEVs infect host cells (often blood cells known as hemocytes) and, like venom, their activity induces changes in host development, nutritional physiology, and/or immunity. DEVs are unable to replicate in host cells but can continually produce a diverse range of proteins involved in host manipulation, which may have longer-term benefits compared to venom; particularly advantageous for koinobiont endoparasitoids. The functions of protein components of venom or those produced by endogenous viruses (virulence proteins) have been described for

several parasitoid species. Outside of these few representative species, little is known about the specific proteins responsible for host phenotypes. Teratocytes and endogenous viruses represent just two types of adaptations of several used to protect or promote parasitoid eggs or larvae in host insects.

Why so many species?

Parasitoid wasps are among the most diverse organisms on the planet, and the reason for their immense diversity is an active area of research. Insects are the primary hosts for most parasitoid wasps, and thus the sheer diversity of insect hosts (approximately one million described species) supports a wide diversity of wasp species. Most parasitoid wasps specialize on just one or a few related host species, and each insect host species may provide a resource for multiple different parasitoid species. In one study, it was estimated that each insect host may support an average of three or four different parasitoid species. Wasps may specialize on a specific life stage of that host, on a different generation within a given year, only attack that host in a portion of its geographic range, or only attack the host if it eats a specific plant. These diverse strategies allow different wasp species to exploit the same host species, and this surely accounts for a major component of parasitoid diversity. Further, as hosts themselves speciate, they are often followed by their wasp hunters who may co-evolve and speciate in turn.

Parasitoids typically have smaller population sizes as they are upper-trophic-level organisms. Thus, genetic drift is likely a prominent evolutionary process and may contribute to reduced hybrid viability and thus facilitate speciation. Female control over the sex of their offspring can allow for quick changes in sex ratio and thus control population size through time, where more females lead to faster population growth. As mentioned, reproductive manipulation by symbionts can prevent hybrids and thus promote speciation. Further, maternally inherited symbionts may limit male progeny, which may help recovery when population numbers

are low, a strategy that can ensure long-term survival of the wasp and, by extension, the symbiont. Finally, parasitoid microbes may also decrease hybrid viability and further promote speciation, but studies are limited. Which of these or other processes explains wasp biodiversity remains to be discovered, and likely all of the above mechanisms have contributed to the astounding diversity of parasitoid wasps.

Conclusions

Despite their diversity, ubiquitous nature, and beneficial status, parasitoid wasps have received far less attention than more charismatic insects such as butterflies and bees. Understanding how and why these wasps have come to be so diverse informs evolutionary theory, patterns of speciation and extinction, and community-interaction dynamics. Further, as we understand parasitoids better, including how they locate and overcome host defenses, we can better use these wasps to help control pests within our gardens, field crops, forests, and greenhouses. By conserving and enhancing our native parasitoid populations, pest populations are less likely to spiral out of control causing devastating crop losses or the need for excessive chemical control. But these tactics require detailed knowledge on which species exist and which specific hosts they attack — foundational science that is still deficient for most parasitoid wasps. But beyond their beneficial use to humans, parasitoid wasps are truly fascinating creatures that display a wide array of strategies to locate, attack, live-off of, and eventually kill their hosts. The most current research seeks to understand the evolution of these traits that are uniquely adapted for efficient utilization of other organisms. From venoms to developing teratocytes to harnessing viruses within their own genomes, parasitoid wasps have truly mastered host exploitation. Meanwhile, the number and diversity of symbionts and pathogenic microbes that are helping or exploiting parasitoid wasps is little known — leaving the field of parasitoid research a fertile arena for scientific discovery for decades to come.

DECLARATION OF INTERESTS

The authors declare no competing interests.

FURTHER READING

- Asgari, S., and Rivers, D.B. (2011). Venom proteins from endoparasitoid wasps and their role in host-parasite interactions. *Annu. Rev. Entomol.* 56, 313–335. <https://doi.org/10.1146/annurev-ento-120709-144849>.
- Austin, A., and Dowton, M., eds. (2000). *Hymenoptera: Evolution, Biodiversity and Biological Control* (Victoria, Australia: CSIRO Publishing).
- Blaimer, B.B., Santos, B.F., Cruaud, A., Gates, M.W., Kula, R.R., Mikó, I., Rasplus, J.Y., Smith, D.R., Talamas, E.J., Brady, S.G., and Buffington, M.L. (2023). Key innovations and the diversification of Hymenoptera. *Nat. Commun.* 14, 1212. <https://doi.org/10.1038/s41467-023-36868-4>.
- Burke, G.R., Hines, H.M., and Sharanowski, B.J. (2021). The presence of ancient core genes reveals endogenization from diverse viral ancestors in parasitoid wasps. *Genome Biol. Evol.* 13, evab105. <https://doi.org/10.1093/gbe/evab105>.
- Charnov, E.L., Los-den Hartogh, R.L., Jones, W.T., and van den Assem, J. (1981). Sex ratio evolution in a variable environment. *Nature* 289, 27–33. <https://doi.org/10.1038/289027a0>.
- Dicke, M., Cusumano, A., and Poelman, E.H. (2020). Microbial symbionts of parasitoids. *Annu. Rev. Entomol.* 65, 171–190. <https://doi.org/10.1146/annurev-ento-011019-024939>.
- Drezen, J.-M., Bezier, A., Burke, G.R., and Strand, M.R. (2022). Bracoviruses, ichnoviruses, and virus-like particles from parasitoid wasps retain many features of their virus ancestors. *Curr. Opin. Insect Sci.* 49, 93–100. <https://doi.org/10.1016/j.cois.2021.12.003>.
- Forbes, A.A., Bagley, R.K., Beer, M.A., Hippee, A.C., and Widmayer, H.A. (2018). Quantifying the unquantifiable: Why Hymenoptera, not Coleoptera, is the most speciose animal order. *BMC Ecol.* 18, 21. <https://doi.org/10.1186/s12898-018-0176-x>.
- Hawkins, B.A. (1993). Refuges, host population dynamics and the genesis of parasitoid diversity. In *Hymenoptera and Biodiversity*, J. LaSalle and I.D. Gauld, eds. (Wallingford, Oxford, UK: C.A.B. International), pp. 235–256.
- Memmot, J., and Godfray, H.C.J. (1994). The structure of a tropical host-parasitoid community. *J. Anim. Ecol.* 3, 521–540. <https://doi.org/10.2307/5219>.
- Pennacchio, F., and Strand, M.R. (2006). Evolution of developmental strategies in parasitic Hymenoptera. *Annu. Rev. Entomol.* 51, 233–258. <https://doi.org/10.1146/annurev.ento.51.110104.151029>.
- Quicke, D.J.L. (1997). *Parasitic Wasps* (London: Chapman and Hall).
- Strand, M.R. (2014). Teratocytes and their functions in parasitoids. *Curr. Opin. Insect Sci.* 6, 68–73. <https://doi.org/10.1016/j.cois.2014.09.005>.
- Tumlinson, J.H. (2023). Complex and beautiful: Unraveling the intricate communication systems among plants and insects. *Annu. Rev. Entomol.* 68, 1–12. <https://doi.org/10.1146/annurev-ento-021622-111028>.

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Trajectory of increased iceberg kill-off in West Antarctica's shallows

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Compared with low latitude coasts, many polar latitudes are still little impacted by intense and direct anthropogenic stressors. Climate forcing is now bringing rapid physical change to nearshore polar realms. In the shallow coastal waters adjacent to the United Kingdom's Rothera Research Station in the West Antarctic Peninsula (WAP), 225 seabed markers at 5–25 m depth have been surveyed and replaced every year from 2002–2023 (75 markers at each of 5, 10 and 25 m). This is one of the longest continuously running marine disturbance experiments in the world, in one of Earth's fastest changing environments. Different categories of sea ice are recorded (including when the sea surface freezes into fast ice) at Rothera since the 1980s, and losses of marine ice in both polar regions are one of the striking responses to a warming planet¹. Five to ten years of seabed marker hit rate data (marker broken or moved) showed that reduced sea ice cover is correlated with disturbance and mortality on the seabed^{2,3}.

Now that this long-term monitoring has yielded 20 years of sea ice-iceberg hit data, it is clear that such a trend is robust enough to hindcast and forecast. Sea ice duration was recorded from the 1980s to present and hindcasting seabed disturbance rates to correspond to these values suggests that more than twice the area of shallow coastal seabed is now catastrophically scoured by icebergs (Figure 1). Projecting the trend forward suggests that in just two decades there may be little or no seasonal fast ice in this area and that on average half the seabed may be hit by icebergs every year.

Iceberg collisions with the seabed (scour) are one of the most frequent natural catastrophic events⁴. Iceberg scour rate is influenced by the duration

