Parasitoid

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A **parasitoid** is an organism that spends a significant portion of its life history attached to or within a single host organism in a relationship where the host is ultimately killed. Thus, parasitoidy is a similar evolutionary strategy to typical parasitism, except for the more serious prognosis for the host.

There are parasitoids in a wide variety of taxa, including microbial diseases, plants, crustaceans, insects, and vertebrates. Especially among the Hymenoptera, ichneumons and many wasps are highly specialised for a parasitoidal way of life. Some parasitoidal wasps are used in biological pest control.



A parasitoidal wasp ovipositing into the body of a spotted alfalfa aphid

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History

The term "parasitoid" was coined in 1913 by the Swedo-Finnish writer Odo Morannal Reuter,^[1] and adopted in English by his reviewer, William Morton Wheeler.^[2] Reuter used it to describe the strategy where the parasite develops in or on the body of a single host individual, eventually killing that host, while the adult is free-living. Since that time, the concept has been variously generalised and widely applied.^[3]

Definitions and distinctions

Parasitoidy is one of six major evolutionary strategies within parasitism, the others being parasitic castrator, directly transmitted parasite, trophically transmitted parasite, vector-transmitted parasite, and micropredator.

These are adaptive peaks, with many possible intermediate strategies, but organisms in many different groups have consistently converged on these six.^[4]

Parasitoids eventually kill their host, typically before it can produce offspring. A nonlethal parasitic organism, especially if it is a fungus, is sometimes termed a biotroph, while a parasitoidal fungus may be called a necrotroph.^{[5][6]}

Idiobiont parasitoids prevent further development of the host after initially immobilizing it, and develop outside the host. Koinobiont parasitoids allow the host to continue its development while feeding upon it, and may parasitise any host life stage.^[7]

There is no clear separation between conventional parasitism and parasitoidy. Many species of true parasites can cause the death of their host if for example they are present in overwhelming numbers or the host is in poor condition, or other compromising circumstances develop, such as secondary infections. For example, blood-sucking



Various endoparasitoids of the moth *Phauda flammans*

mites sometimes overwhelm nestlings of birds such as swallows to the point that the young birds cannot fledge successfully,.^[8]

In their extreme forms, conventional parasitism and parasitoidy are distinct: there is no doubt that the larva of a Tarantula hawk wasp behaves more like a parasitoid, or even a predator, than a parasite; and similarly the biting midges that suck blood from large insects are plainly ectoparasites; but many intermediate forms exist. At the opposite extreme, parasitoidy grades into predation. Differences between various hunting wasps provide convenient illustrations. Predatory social wasps hunt flies, caterpillars and the like, grab them, butcher them, carry them home and feed them to their young. Similarly, some solitary wasps such as beewolves, sting prey, sometimes fatally, before saving it, usually entire, in a nest or burrow for the young to feed on. In contrast, the best-known protelean solitary hunting wasps sting prey to paralyse it before storing it for the young in the nest. [9][10] Other wasps paralyse prey in the plant or other environment in which it feeds, before laying eggs nearby; the emerging young feed on the paralysed prey in its own home. [11] Some insect parasitoids lay their eggs where the larvae must locate the prey for themselves when they hatch from the eggs. [12] Examples include flies in the families Tachinidae and Bombyliidae, often with sophisticated physiological and strategic adaptations.

Influence on host behaviour

In another strategy, some parasitoids influence the host's behaviour in ways that favour the propagation of the parasitoid, often at the cost of the host's life. A spectacular example is the lancet liver fluke that causes host ants to die clinging to grass stalks, where grazers or birds may be expected to eat them and complete the parasitoidal fluke's life cycle in its definitive host. Similarly, as strepsipteran parasitoids of ants mature, they cause the hosts to climb high on grass stalks, positions that are risky, but favour the emergence of the strepsipterans. Other species of endoparasitoids cause infected woodlice and land Amphipoda such as *Talitroides* to run about in the open by day, where predators such as birds can catch them and continue the cycle. The rabies virus affects the host's central nervous system, eventually killing it, but perhaps helping to disseminate the virus by modifying the host's behaviour. The paralysis inflicted by soft ticks might be seen as influencing behaviour, preventing the host from wandering away while they feed.

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In different taxa

Microbial diseases

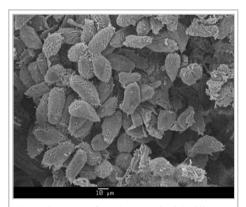
Some microbial parasitoids waste most of the host's resources when it dies, but others exploit the host efficiently. Microbial pathogens of insects include microsporidiosis in the form of nosema in silkworms. This infection is highly virulent^[16] and the tissues of the victims contain huge numbers of infectious spores. In effect the pathogen in its role of parasitoid has used up most of the resources of the host to propagate and spread its offspring. Similarly, many viruses propagate inside a host cell until it physically ruptures. Parasitoidal fungi such as Entomophthora species carry this principle as far as is possible. Having infected and killed an insect, they continue to grow on the carcase and release spores for as long as any resources remain.

Female *Apocephalus borealis* ovipositing into the abdomen of a worker honey bee

Plants

Parasitoidal plants include various species of dodder, which indiscriminately parasitise wide ranges of host plants, and debilitate or kill the branches that they infect, and commonly the whole host plant as well.^{[4][17]}

Mistletoes in families such as Santalaceae and Loranthaceae commonly accumulate on host trees until they stunt and eventually kill them, sometimes after many decades. Occasionally a freak condition can arise where the (strictly speaking "hemiparasitic") plant can supply sufficient photosynthetic power to support the root system of a small host tree for several years after the live host shoots have effectively disappeared.^[18]



SEM image of endoparasitoid ciliates of the genus *Collinia*, which can cause mass mortality in krill

A related example is where the parasitoid plant is not strictly a parasite in the normal sense, but nonetheless exploits the host's resources of space, support and light. The best-known are the so-called "strangler figs". Some of them grow on and around the trunk of the host tree and squeeze or starve it of light until, after perhaps decades, it dies. The strangler eventually replaces the host utterly as the original trunk rots within the stems of the strangler, leaving a hollow framework. [4][19]

Crustaceans

The many parasitoidal Crustacea have a wide range of species and strategies. The killing of the host is often incidental. In the gill lice, most adult females live as parasites in the gills of fish, causing incidental harm that may kill the fish or weaken them so badly as to prevent breeding. *Sacculina* barnacles inject themselves into a crab, and convert themselves into egg-laying bags. This disrupts the crab's reproductive system in parasitic castration.^[20]

Insects

About 10% of described insect species are parasitoids^[21] in four insect orders, but far the majority are in the Hymenoptera. The largest group comprises the so-called "Parasitica" within the Hymenopteran suborder

Apocrita: most of these are chalcidoid wasps and ichneumon wasps, followed by the Proctotrupoidea and Platygastroidea. Outside these, many other Hymenopteran lineages include parasitoids, such as most of the Chrysidoidea and Vespoidea, the rare Symphytan family Orussidae, and *Elasmus polistis*, *which parasitises* Polistes exclamans.^[22]

The flies (order Diptera) include several families of parasitoids, the largest of which is the Tachinidae, along with the Pipunculidae, Conopidae and others. Other families of flies include some protelean species. For example, Phoridae have already been mentioned as parasitoidal on ants, and some flesh fly species, such as *Emblemasoma auditrix*, are parasitoidal on cicadas, locating their hosts by sound.^[23]



Braconidae wasp cocoons on giant leopard larva

The "twisted-wing parasites" (Strepsiptera) consists entirely of parasitoids which usually sterilise their host. Two beetle families, Ripiphoridae and Rhipiceridae, are largely parasitoids, as are *Aleochara* rove beetles. Other orders include a few parasitoids, such as epipyropid moths, which are ectoparasitoids of planthoppers and cicadas. More elaborately, the genus *Cyclotorna* begins its growth period parasitising plant bugs, and ends by feeding on ant larvae in their colonies.

Hymenopteran parasitoids often have unique life cycles. In one family, the Trigonalidae, the female wasps deposit eggs into small pockets they cut into the edge of leaves with their ovipositor. A caterpillar chewing these leaves may unknowingly swallow some of the eggs, and when they get into the caterpillar's gut, they hatch and burrow through the gut wall and into the body cavity. Later they search the caterpillar's body cavity for other parasitoid larvae, and it is these they attack and feed on. Some trigonalids, once in a caterpillar or sawfly larva, need their vehicle to fall prey to a social wasp. The wasp carries the caterpillar back to its nest, and there it is butchered and fed to the wasp's young; they will serve as the host for the trigonalid, the eggs of which are in



Koinobiont parasitoid on moth larva

the butchered caterpillar.^[24] Another example is an Ichneumon wasp, *Ichneumon eumerus*, which parasitises the butterfly *Phengaris rebeli* by directly seeking out, through smell, Myrmica ant nests that the butterfly larvae previously parasitised, and ovipositing into the *P. rebeli* larvae.^[25] Once the wasps' eggs hatch, they feast on the carcass of the dead caterpillar.

Vertebrates



Sea lamprey, Petromyzon marinus

Lampreys can be either parasitic or parasitoidal. Most species are not parasitic, but among the North American species for example, several are ectoparasitic on freshwater fishes. They rasp away the skin of the host and suck the blood, but most do only superficial damage. In contrast, the sea

lamprey inflicts deep rasping wounds, and the muscle damage and loss of blood commonly weaken the host severely, affecting its reproduction or killing it.

The sabre-toothed blenny parasitises the cleaning symbiosis relationship between some cleaner fish and their client fishes. It attacks the client fish, approaching it in the guise of cleaner wrasse, and snatches a mouthful of

scales or other convenient tissue. Clients often react violently, and thereafter trust neither wrasse nor the wrasse-mimicking blenny.

Another form of parasitism that can approach parasitoidy occurs in the Perissodini, cichlids from Lake Tanganyika. Seven species in the genus *Perissodus* are specialised in eating scales from other fish. Their teeth are variously suited to being able to grab bits of skin with the scales attached. At least some of the species also have adaptations in their behavior to enable them to approach potential hosts.^[26] They have an adaptation of the jaw that enables them to lash out sideways when passing a victim; the jaw is asymmetrical,^[27] and there is continuous selection for the asymmetry that currently is less frequent in the population, because host fishes are more alert to defend themselves on the side on which they have been attacked in the past.^[28]

Such a lifestyle is reminiscent of sharks of the genus *Isistius*, also known as the cookiecutter shark because of the circular wounds it leaves on the skin of whales and large fish that it has bitten in passing.^[29] *Isistius* species have been referred to as partly ectoparasitic,^[30] but they sometimes overwhelm their hosts and kill them, which by definition amounts to parasitoidy.

Candiru and related fishes in the family Trichomycteridae, subfamilies Vandelliinae and Stegophilinae, present unusual examples of vertebrate parasitism, and occasionally parasitoidy. Candiru can enter the human urethra and other orifices, but they are very varied in their habits. Some burrow partway into the skin of larger fish, apparently largely for protection and transport rather than food. Several are haematophagous, commonly entering the gill cavities of larger fishes and feeding on blood drawn from the gill filaments. At least when large fishes are tethered by fishermen where large numbers of the parasites occur, the hosts may die.

Among birds, brood parasitism is found in the cuckoos, honey-guides, cowbirds and other groups. They are parasitoids, as they often cause the starvation of the host's chicks by competing with them for food, while others either remove host eggs when laying eggs in host nests (sometimes eating the eggs removed), or the chick ejects or kills the eggs or chicks of the host when they hatch. Some hatchlings have hooked beaks adapted to attacking the host chicks and eggs; these hooks vanish before fledging.

Wasp parasitoidal oviposition

Oviposition is a process which is complex, as it not only depends on finding the specific host and certain environmental conditions, but also on evading the different types of host defense mechanisms. There are parasitoidal plants, crustaceans, insects and vertebrates. Among parasitoidal insects, parasitoidal wasp oviposition is a topic that has been studied thoroughly.

Parasitoidal wasps are classified under the order Hymenoptera, suborder Apocrita and infraorder Parasitica.^[31] Parasitoidal wasps can be classified as either endoparasitic or ectoparasitic according to the locations where they lay their eggs.^[32] Endoparasitic wasps insert their eggs inside their host, while ectoparasitic wasps lay theirs outside the host body.^[33]

Parasitoid wasps have a different range of obstacles that have to be overcome in order to successfully oviposit inside or on their hosts, according to their endoparasitic or ectoparasitic nature.^[33] These barriers include behavioral, morphological, physiological or immunological defenses.^[34] An example of immunological defense towards endoparasitic wasps would be the encapsulation of their eggs.^[35] To thwart this immunological protection system, wasps inundate their host with their eggs so as to overload the encapsulation response.^[36] Another way of hindering a host's defense is to introduce a virus which interferes with the development of defenses.^[37]

Parasitoid wasps are able to locate hosts by detecting certain indirect plant defense mechanisms against insect herbivores.^[38] When attacked by insect herbivores, some plants release chemicals which attract parasitoid wasps but do not cause any harm to these predators.^[38] Some wasps insert the ovipositor organ into a host, while other wasps place their eggs onto a host egg. The ovipositor is a relatively long tube-like organ used to inject eggs into hosts.^[31] This organ consists of the genital structures that are made from segments eight and nine of the wasp's body.^[31]

Once the host has been located, the wasp either uses the horizontal or vertical alighting approach from behind.^[39] In the horizontal method, the wasp maintains its body horizontally until it grabs on to the ant's metasoma (upper abdomen) with its tarsi (lower legs). After that, it places the rest of its legs on the ant's abdomen, folds its wings, and proceeds to inject its victim with the ovipositor.^[39] The vertical approach is more complicated, and requires more steps. The wasp attaches its front legs onto the ant's abdomen, then rotates 180 degrees so that it becomes upside down.^[39] After that, it rotates once more so that its head and legs switch places, before inserting its ovipositor.^[39]

Ants are often aware of the wasps' presence, as they violently turn around, moving their mandibles and legs in order to defend against their attacker. This example of behavioral defense displayed by ants is not unusual, and sometimes prevents the wasps from depositing their eggs successfully.^[32] To try to beat such behavioral diversions, the wasps close in very fast to inject their hosts.^[40] To prevent missing the target when making contact with the host, the wasp may wait for the ant to stop moving, and then attack suddenly.^[40]



Megarhyssa macrurus, a parasitoid, ovipositing into its host through the wood of a tree. The body of a female is c. 2 inches (51 mm) long, with an ovipositor c. 4 inches (100 mm) long.

Biological control

Parasitoids are among the most widely used biological control agents. From the point of view of the farmer or horticulturalist, the most important groups are the Ichneumonid wasps, which prey mainly on caterpillars of butterflies and moths; Braconid wasps, which attack caterpillars and a wide range of other insects including greenfly; Chalcid wasps, which parasitise eggs and larvae of greenfly, whitefly, cabbage caterpillars, and scale insects; and Tachinid flies, which parasitize a wide range of insects including caterpillars, adult and larval beetles, and true bugs.^[41] Commercially, there are two types of rearing systems: short-term daily output with high production of parasitoids per day, and long-term low daily output with a range in production of 4-1000 million female parasitoids per week.^[42] Larger production facilities produce on a yearlong basis, whereas some facilities produce



Encarsia formosa, bred commercially to control whitefly in greenhouses

only seasonally. Rearing facilities are usually a significant distance from where the agents are to be used in the field, and transporting the parasitoids from the point of production to the point of use can pose problems.^[43] Shipping conditions can be too hot, and even vibrations from planes or trucks can adversely affect parasitoids.^[42]

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See also

■ Parasitoid wasp

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External links

- On the UF / IFAS Featured Creatures website:
 - *Ageniaspis citricola*, a citrus leafminer parasitoid (http://entomology.ifas.ufl.edu/creatures /beneficial/a_citricola.htm) (Insecta: Hymenoptera: Encyrtidae)
 - Amitus hesperidum, a citrus blackfly parasitoid (http://entomology.ifas.ufl.edu/creatures/beneficial/amitus_hesperidum.htm) (Insecta: Hymenoptera: Platygastridae)
 - *Cirrospilus ingenuus*, a citrus leafminer parasitoid (http://entomology.ifas.ufl.edu/creatures /beneficial/cirrospilus_ingenuus.htm) (Insecta: Hymenoptera: Eulophidae)
 - *Encarsia lahorensis*, a citrus whitefly parasitoid (http://entomology.ifas.ufl.edu/creatures /beneficial/encarsia_lahorensis.htm) (Insecta: Hymenoptera: Aphelinidae)

- *Encarsia opulenta*, a citrus blackfly parasitoid (http://entomology.ifas.ufl.edu/creatures/beneficial /encarsia_opulenta.htm) (Insecta: Hymenoptera: Aphelinidae)
- *Lipolexis scutellaris*, brown citrus aphid parasitoid (http://entomology.ifas.ufl.edu/creatures /beneficial/bca_parasitoid.htm) (Insecta: Hymenoptera: Aphidiidae)
- *Semielacher petiolatus*, a citrus leafminer parasitoid (http://entomology.ifas.ufl.edu/creatures /beneficial/s_petiolatus.htm) (Insecta: Hymenoptera: Eulophidae)
- *Steinernema scapterisci*, mole cricket nematode (http://entomology.ifas.ufl.edu/creatures /nematode/mole_cricket_nematode.htm) (Nematoda: Rhabditida: Steinernematidae)
- Parasitic and Parasitoid Alien Species in Science Fiction Movies (http://www.explore-science-fiction-movies.com/parasiticparasitoidalienswikipedia)

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