NATURAL HISTORY OF TROPICAL PARASITOID WASPS

M. O. Gonzaga
Instituto de Biologia, Universidade Federal de Uberlândia

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Summary

The order Hymenoptera currently includes the impressive number of more than 115000 known species. The tropical hymenopteran fauna, however, is poorly known and this number probably represents just a small fraction of the real richness of the group. A great part of the species within Hymenoptera is composed of parasitoids, animals that exploit other organisms to death in order to acquire the food resources required to their development. Here I present a brief overview of the natural history of these interesting animals, focusing on the interactions with their hosts. I also present details of some study cases in a few families to illustrate the diversity of the behaviors within the group. Finally, I describe some cases in which the interactions with the hosts culminate with changes in their normal behaviors, increasing the survivorship of the manipulative parasitoids

1. What is a Pparasitoid?

The term parasitoid was coined by O.M. Reuter, about one century ago, to describe particular feeding habits presented by some insects. Those organisms spend part of their lives consuming another animal, the host, living within or attached to its body. In most of them, the larval stages exploit arthropod hosts (dipterans, however, exploit a wide range of hosts, including flat-worms, several groups of arthropods and even toads). The difference between parasitoids and parasites lies in the final consequence for the organism attacked. Parasites consume part of the food resources and/or some tissues of

the host, but their action rarely causes the host's death. Death usually happens only in particular cases, when the parasite load is exceptionally high. Hosts attacked by parasitoids, on the other hand, are invariably condemned. The adult parasitoids are free-living organisms, consuming other resources, such as flowers and honeydew.

Some authors use the term "parasitoid" for all those organisms that kill their single host after completing their development on it. This definition is wide enough to include some hunting wasps of the family (Pompilidae) (Figure 1A). Part of the species of Pompilidae attacks wandering spiders, laying an egg on their bodies after inducing a temporary paralysis. When the effect of the venom wears off, the spider can continue its activities during most of the development of the wasp larva. Others, such as the Japanese species *Homonotus iwatai*, invade spider's lairs, deposit one egg on the host's body and leave the site. The egg hatches in 2-3 days after the attack and about a week later the spider will be completely consumed by the larva. Most species in Pompilidae, however, capture a single spider and deposit this prey in a mud nest attached to the surface of sheltered substrates or in a nest created by changing a natural cavity or by the excavation of a new one. The permanent paralysis and transportation of the host after the interaction with the female wasp are the characters used to place those species in a different category, the "provisioning predators". By transporting the host to a protected site these wasps possibly reduced the susceptibility of their larvae to predators and/or hyperparasitoids, which are parasitoids of parasitoids. Transportation also probably was an important factor determining the ability of some wasp families to provide many prey items to their young. This behavior is characteristic of the families Sphecidae and Crabronidae (Figure 1B), for example. While pompilids offer a single prey to each larva, sphecids and crabronids, usually store several relatively small spiders (and also other groups of prey, depending on the wasp species) in each cell of their nests.

Figure 1. A. *Pepsis* sp. (Pompilidae) depositing a large spider (Theraphosidae) in her nest. B. *Trypoxylon albonigrum* (Crabronidae) constructing a mud nest to store several small orb-web spiders which will be consumed later by her brood. Photos: M. O. Gonzaga

Most parasitoids are distributed in four orders of Insecta: Hymenoptera (about three-quarters of all parasitoids), Diptera, Strepsiptera and Coleoptera. A few species are also

known among Neuroptera, Lepidoptera and Trichoptera. The parasitoid lifeway has arisen only once in Hymenoptera and evolved independently at least 21 times in Diptera and 11 times in Coleoptera. The current number of parasitoid species described within these orders is about 68,000, but this number may represent only 8.5% of the parasitoid species that actually live in our planet. Considering that most parasitoid groups are poorly known, especially in the tropics, some researchers have estimated that the number of parasitoids species on Earth may reach 1.6 to 2 million. Among them there is a great variety of life histories and some amazing adaptations, such as the manipulation of host's behavior in order to increase the parasitoid survivorship during specific stages of their development.

In this brief overview of natural history of tropical parasitoid wasps I will focus on general aspects of the behavior (especially regarding the interaction with hosts) and life histories of the most studied groups. I will also mention some examples of study cases to highlight the great diversity of habits of those hymenopterans. Finally, I intent to present some particular and interesting details of the life of some wasps, such as the host behavioral manipulation registered in interactions between the larvae of ichneumonid parasitoids and their spider hosts.

2. Life Histories

Parasitoids can be divided in two major groups according to their life-history strategies, the koinobionts and the idiobionts. The first group includes species that attack mobile and growing host stages, developing over a prolonged period within the live host or attached on the external surface of the host's body. As the host continues to perform its normal activities, including those related to avoid predators, the parasitoid remains protected and is able to exploit the resources acquired by the host during the association. The idiobionts, on the other hand, paralyze or kill their hosts (usually immobile stages, such as eggs or pupae or arthropods living in concealed or protected sites). By killing the host, female wasps restrict the food available to their larvae to the resources already present in the host's body at the moment of its selection. In those cases, the parasitoid safety depends completely on the host's own concealment and/or the barrier provided by its cuticle.

Hymenoptera parasitoids may develop within (endoparasitoids) or attached to their host's bodies (ectoparasitoids). Feeding externally on the hosts is probably the ancestral way to obtain food for the carnivorous larvae of this group. Some species, however, spend their first instars attached to the surface of their host's bodies and then burrow a cavity to become endoparasites. Others, such some of the genus *Meteorus* (Braconidae) do the opposite. They live the first instars inside their hosts and then leave to pupate, remaining attached to the host or vegetation by a series of silk lines (Figure 2). Finally, some parasitoid wasps spend all the maturation process protected inside their hosts. Most aphidiine (Braconidae) (Figure 3), for example, consume their aphid (Hemiptera) hosts from inside and also pupate within their mummified bodies.

Most koinobiont species are endoparasitoids. They usually insert the ovipositor into the host, injecting venom and the egg, without promoting serious injuries. This is important because the security of the parasitoid offspring depends on the future activity and

integrity of the host. Some koinobionts, however, are ectoparasitoids. This is the case, for example, of the several genera of the family Ichneumonidae that attack spiders. The wasps of those species attach an egg on the cephalothorax or abdomen of their hosts and the developing larva perforates the spider's body to drink the haemolymph. Among idiobionts, the ectophagous strategy is more frequent. Females of idiobiont species also use venom in attack, sometimes killing the host and sometimes just immobilizing. The immobilization of the host prevents any attempts to dislodge or injure the fragile egg deposited by the wasp.

Figure 2: Cocoons of *Meteorus* sp. (Hymenoptera: Braconidae: Meteorinae) attached to the body of a larva (Lepidoptera: Sphingidae). Photo: M. O. Gonzaga.

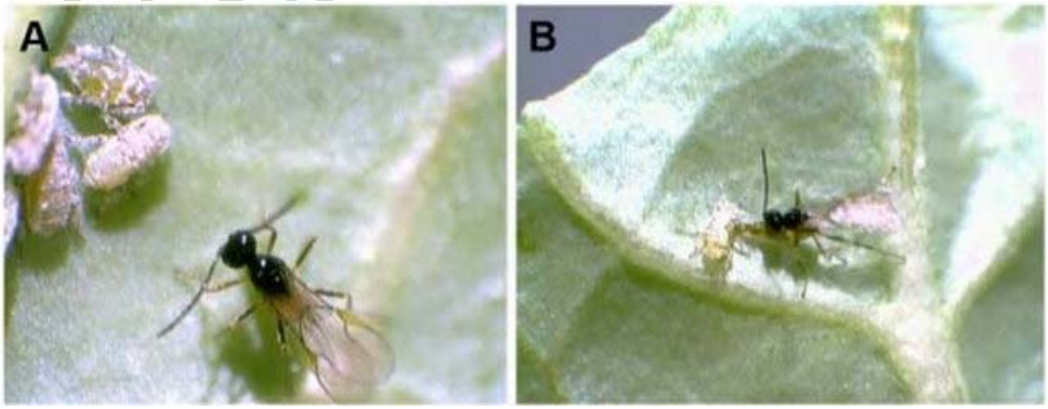

Figure 3: Female of the parasitoid *Diaeretiella rapae* (Hymenoptera: Braconidae, Aphidiinae) attacking its host, the cabbage aphid *Brevicoryne brassicae* (Hemiptera: Aphididae). *Diaeretiella rapae* is primarily attracted to cruciferous plant odors. The

female lays one egg directly into the host's body. After the attack, the host remains at the same site, feeding normally for about four days. During this interval the parasitoid larva is slowly eating the host's internal tissues. The wasp pupates within the host's body and emerges from the mummy as an adult. Photos: M. V. Sampaio.

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Biographical Sketch

Marcelo O. Gonzaga has a degree in Biological Sciences from Universidade Federal de Minas Gerais (1996), master and doctor degrees in ecology from Universidade Estadual de Campinas (1999 and 2006). He was an associated researcher in the Departamento de Ecologia e Biologia Evolutiva da Universidade Federal de São Carlos and Fellow of the Program for Young Researchers of FAPESP. Part of his currently projects involves the measurement and analysis of the interactions between parasitoid wasps and egg predators and their hosts. He is also working about host behavioral manipulation in systems involving spiders of the families Araneidae, Tetragnathidae and Nephilidae and their ichneumonid parasitoids. He has experience in the field ecology, with emphasis on behavioral ecology. He was recently hired by the Institute of Biology of Universidade Federal de Uberlândia and is affiliated to Post-graduate course in Ecology and Conservation of Natural Resources.