

Trichogramma Wasps *Trichogramma* spp. (Insecta: Hymenoptera: Trichogrammatidae)¹

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Introduction

Trichogramma is a genus of wasps that includes approximately 145 described species, all of which are insect egg parasitoids (Knutson 1998). This means that adult female *Trichogramma* wasps deposit eggs within the eggs of other insects, which hatch into larvae and feed on the host egg from within. These wasps primarily use moth and butterfly (Lepidoptera) eggs as hosts, but also those of beetles (Coleoptera), flies (Diptera), true bugs (Hemiptera), grasshoppers and crickets (Orthoptera), dragonflies (Odonata), other wasps (Hymenoptera), lacewings (Neuroptera), and thrips (Thysanoptera). Many hosts that *Trichogramma* wasps attack are economically important plant pests, making this group of wasps a valuable biological control agent (Flanders and Quednau 1960, Smith 1996). *Trichogramma* wasps are considered among the most important parasitoid natural enemies of insect pests. However, naturally-occurring *Trichogramma* populations in cropping systems are often not adequate to reduce pest populations below damaging levels. Therefore, field populations of *Trichogramma* are often augmented with insectary-cultured

individuals, which can be purchased commercially. *Trichogramma* wasps have been released to control various economic pests of agronomic and fruit crops since the late 1970s (Hassan 1993).

Description

Due to the small size of *Trichogramma* wasps, they are difficult to identify on-site and without substantial magnification. Some physical characteristics such as body color, length, and the number of body hairs vary depending on body size, season, host, and environmental conditions like temperature. Fragile body structures and loss of curated reference wasp specimens (type specimens collected and stored in museums or university collections) has resulted in many misidentifications of species in the family Trichogrammatidae (Pinto et al. 1983, Pinto and Stouthamer 1994, Knutson 1998, Sumer, et al. 2009).

There are 30 described *Trichogramma* species in North America. The most commonly collected species in orchards and other agronomic crops in North America are *Trichogramma atopovirilia* Oatman and Platner, *Trichogramma brevicapillum* Pinto and Platner, *Trichogramma deion* Pinto and Oatman, *Trichogramma exiguum* Pinto & Platner, *Trichogramma fuentesi* Torre, *Trichogramma minutum* Riley, *Trichogramma brassicae* Bezdenko, *Trichogramma nubilale* Ertle and Davis, *Trichogramma platneri* Nagarkatti,

1. This document is IN1382 one of a series of the Entomology and Nematology Department, UF/IFAS Extension. Original publication date October 2022. Visit the EDIS website at <https://edis.ifas.ufl.edu> for the currently supported version of this publication. This document is also available on the Featured Creatures website at <http://entomology.ifas.ufl.edu/creatures>.
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Trichogramma pretiosum Riley, and *Trichogramma thalense* Pinto and Oatman (Knutson 1998, Orr et al. 1999, Orr et al. 2000, LeBeck and Leppla 2021).

Trichogramma fuentesi, among the most commonly observed species in this genus, is native to the USA, Mexico, Peru, Barbados, Argentina, Venezuela, and Cuba (Pinto et al. 1983, Rodriguez et al. 1994, Zucchi et al. 2010). Within the United States, it has been found in Alabama, California, New Jersey, South Carolina, Florida, Texas, and Louisiana (Paraiso et al. 2012). *Trichogramma fuentesi* can be found in most annual crop and fruit tree habitats (Zucchi et al. 2010).

Life Cycle

Trichogramma spp. undergo complete metamorphosis, which includes four life stages: egg, larva, pupa, and adult. The time from egg to adult lasts seven to ten days and usually have more generations per year than their hosts. The life cycle can vary in length and could last more than 10 days due to unfavorable environmental conditions. *Trichogramma* wasps are endoparasitoids, meaning that they complete their development inside their host. An adult female wasp will deposit an egg within a viable egg of another insect, the egg will hatch into a larva, and the larva will consume the host egg from within. After pupating within the egg, a newly developed adult *Trichogramma* wasp will emerge from the host's empty egg case and fly away to parasitize (deposit more eggs) in host eggs (Knutson 1998).

Eggs

Adult female *Trichogramma* wasps drill a tiny hole in a host's recently deposited egg to insert one or more eggs. She will use her ovipositor to chemically mark the host eggs that have already been parasitized. Evidence suggests that females of some *Trichogramma* species also inject venom into the parasitized host egg, which causes predigestion of the egg's contents and facilitates *Trichogramma* larval feeding.

Larvae

Once inside their host egg, *Trichogramma* eggs will hatch into larvae and develop through three larval instars within the host's egg, consuming the embryo and yolk as sources of nutrients. It takes 3-4 days after parasitism for a larva to reach the third and final instar, at which point it deposits dark melanin granules on the inner surface of the host's egg lining (Figure 1, 2).



Figure 1. Corn earworm egg parasitized by a *Trichogramma* spp. The parasitized host egg on the left shows the darkened melanin pigmentation produced by the *Trichogramma* larva within. On the right is an empty previously parasitized host egg casing. Credits: Jack Kelly Clark, courtesy University of California Statewide IPM Program

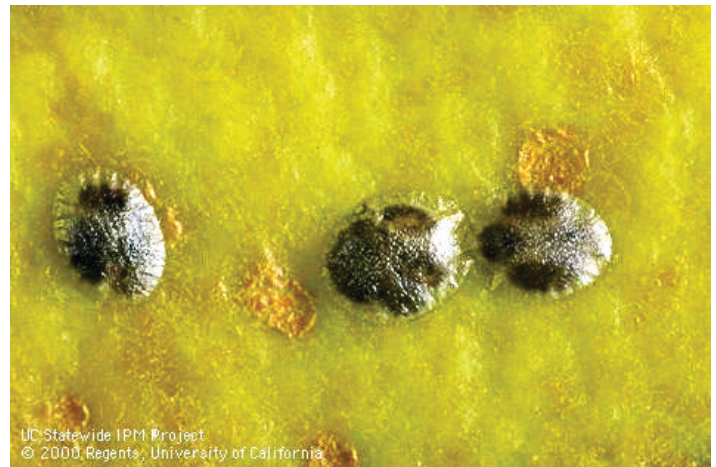


Figure 2. Codling moth eggs turn black when parasitized by *Trichogramma platneri*. Credits: Jack Kelly Clark, courtesy University of California Statewide IPM Program



Figure 3. *Trichogramma* spp. female on the egg of tomato fruitworm, *Helicoverpa zea*. Credits: Jack Kelly Clark, courtesy University of California Statewide IPM Program

Pupae

After completing the third larval instar, *Trichogramma* larvae will have consumed the contents of the host egg and will pupate inside the host egg. Although this insect undergoes multiple generations per year, the pupae may spend cooler winter months within the host's egg, during which they slow their metabolic activity. Overwintering pupae can tolerate and survive subfreezing temperatures during the cold months of the year.

Adults leave the host eggs as they emerge from their pupae. Males emerging from a parasitized host egg will remain at the host egg, awaiting the emergence of nearby adult females to mate with.

Adults

Overwintering pupae tend to emerge from the host's parasitized egg as adults in May and June to attack new host eggs. *Trichogramma* adults are very small (1 mm or less) and have long antennae and small hairs relative to their body size (Figure 3). *Trichogramma* species are morphologically similar, which makes them very difficult to distinguish. Their forewings have distinct sections and venation, while the hindwings are less distinctly veined. As adults, several species, including *Trichogramma fuentesi*, are light yellow or yellow with tallow-brown to black markings. In females, the ovipositor is slightly shorter than the antennae (Pinto et al. 1983, Rodriguez et al. 1994).

Oviposition rate, or the number of eggs deposited per adult female, varies with the age of the adult. Unmated *Trichogramma fuentesi* adult females can still produce viable eggs and usually stop parasitizing after three days as an adult. Mated females tend to stop parasitizing after five days as an adult (Paraiso et al. 2012). Mated adult female *Trichogramma* wasps can determine which eggs are fertilized with male sperm. More specifically, *Trichogramma* species are arrhenotokous, meaning that unfertilized eggs will develop into males and fertilized eggs will develop into females. *Trichogramma fuentesi* adult females prefer to oviposit in younger host eggs, and the sex ratio of its progeny is typically female-biased (Suzuki et al. 1984, Paraiso et al. 2013a). Evidence suggests that many parasitoid wasps, like *Trichogramma* spp., also regulate the sex of their offspring based on the quality of their egg hosts. For example, unfertilized eggs (that develop into males) will be deposited into lower quality host eggs, while fertilized eggs (that develop into females) are deposited in higher quality host eggs (Charnov, et al. 1981).

Adult *Trichogramma* females use kairomones (chemical substances emitted by host organisms) to locate moth eggs. Some of these kairomones are sex pheromones used by hosts to attract mates (e.g., bollworm). Factors such as egg shape, size, color, interior chemical cues, and egg surface chemical characteristics may be used by adult *Trichogramma* wasps in assessing host egg quality and suitability for parasitism. In addition to parasitizing eggs, adult females of many *Trichogramma* species will also consume the eggs of their host to obtain additional nutrients to fuel their egg production (Knutson 1998).

Unlike other species, *Trichogramma fuentesi* does not seem to host feed. Instead, adult females devote more time to searching for hosts and ovipositing (Paraiso et al. 2013a). This strategy suggests that *Trichogramma fuentesi* is pro-ovigenic, meaning that female adults emerge from pupae with all their eggs already developed. However, adult female *Trichogramma fuentesi* can still benefit from foraging on host eggs (Paraiso et al. 2012).

Hosts

Trichogramma wasps are generalist parasitoids, attacking a broad range of diverse host species. Some of the hosts parasitized by *Trichogramma* spp. include tomato hornworm (*Manduca quinquemaculata* Haworth), tomato pinworm (*Keiferia lycopersicella* Walshingham), imported cabbageworm (*Pieris rapae* Linnaeus), diamondback moth (*Plutella xylostella* Linnaeus), Oriental fruit moth (*Grapholita molesta* Busck), codling moth (*Cydia pomonella* Linnaeus), and spongy moth (*Lymantria dispar* Linnaeus) (Knutson 1998).

Trichogramma fuentesi is known to parasitize several moths and butterflies in the families Crambidae, Noctuidae, Pyralidae, Danaidae, Erebidae, and Papilionidae. Most notably, this species attacks several economic pests including tropical sod webworm (*Herphtegamma phaeopteralis* Guenée), Mexican rice borer (*Eoreuma loftini* Dyar), sugarcane borer (*Diatraea saccharalis* Fabricius), cabbage looper (*Trichoplusia ni* Hübner), cactus moth (*Cactoblastis cactorum* Berg), corn earworm/tomato fruitworm/bollworm (*Helicoverpa zea* Boddie), and the tobacco budworm (*Heliothis virescens* Fabricius) (Browning and Melton 1987, Greenberg et al. 1998, Zucchi et al. 2010, Paraiso et al. 2011, Tofangsazi et al. 2014). A few other studied hosts include julia heliconian (*Dryas iulia* Hübner), common buckeye (*Junonia coenia* Hübner), painted lady (*Vanessa cardui* Linnaeus), eastern tiger swallowtail (*Papilio glaucus* Linnaeus), black swallowtail (*Papilio polyxenes* Fabricius), eastern cactus-boring moth (*Melitara prodenialis* Walker),

and the moth species (*Anomis texana* Riley) (Zucchi et al. 2010, Paraiso et al. 2013b).

Economic Importance

Due to their rapid development and broad host range, *Trichogramma* wasps have been considered as commercial biological control agents to help manage economically important insect plant pests. Several *Trichogramma* spp. are reared by private companies and sold for augmentative biological control applications (LeBeck and Leppla 2021). Some companies sell single *Trichogramma* species individually or with a combination of several species. *Trichogramma* mass rearing requires providing host eggs for adult wasps to parasitize, which commonly include the Angoumois grain moth (*Sitotroga cerealella* Olivier) and the Mediterranean flour moth (*Ephestia kuehniella* Zeller), which are themselves reared on wheat and other grain host plants. Despite the widespread availability and efforts, there is some controversy about the effectiveness of *Trichogramma* wasps as biological control agents.

In addition to commercially produced biological control agents, many *Trichogramma* species exclusively occur in nature. For example, *Trichogramma fuentesi* attacks several economically and ecologically important insects. However, this species is not promoted as an augmentation biological control agent. One reason being that *Trichogramma fuentesi* may attack some native non-pest species instead of pests. While investigating *Trichogramma fuentesi* as a biological control agent of the cactus moth (*Cactoblastis cactorum*), Paraiso et al. (2013b) found that parasitism of a native non-target species, *Melitara prodenialis*, was around nine times higher than parasitism of the target pest species. In some systems, this preference to parasitize native non-pest species could harm beneficial species.

Although not a commercially produced biological control agent, *Trichogramma fuentesi* can still be an important natural enemy in some ecosystems. Browning and Melton (1987) surveyed naturally occurring egg parasitoids in Texas sugarcane fields and found *Trichogramma fuentesi* to be the most successful parasitoid of the sugarcane borer *Diatraea saccharalis*, parasitizing 78.7% of eggs. Moreover, releases of *Trichogramma fuentesi* within closed systems, like greenhouses, may be an effective use of this species for augmentative pest management. Although not a greenhouse pest, Tofangsazi et al. (2014) found that *Trichogramma fuentesi* parasitized over 80% of tropical sod webworm eggs in their laboratory colony, demonstrating its value when confined to a single host species (Tofangsazi et al. 2014).

Over the past several decades, there have been multiple introductions of *Trichogramma* wasps into the US for classical biological control of economic pests. These introductions are listed below:

- In 1968, *Trichogramma evanescens* Westwood was introduced from Europe into southern California and Missouri for control of imported cabbageworm and cabbage looper on cabbage (Waage and Ming 1984).
- In 1975, *Trichogramma euproctidis* Girault was introduced from Russia into Georgia for cotton bollworm control on cotton (Knutson 1998).
- In 1993, *Trichogramma bactrae* Nagaraja was introduced from Australia into California and Arizona for control of the pink bollworm in cotton (Knutson 1998).
- In 1993-96, *Trichogramma ostrinae* Pang and Chen was introduced from China into New York for control of European corn borer in sweet corn (Wang et al. 1997).

In addition to the historical introductions of *Trichogramma* species, there are also some species currently used in biological control programs (Cònsoli et al. 2010, LeBeck and Leppla 2021):

Trichogramma minutum—native to North America used for control of grape berry moth, cabbage looper, and codling moth in ornamentals, orchards, grape production, and forests (Greenberg et al. 1998).

Trichogramma platneri—native to North America used for control of codling moth and leafrollers in avocados, ornamentals, orchards, and grape production (Li 1994, Smith 1996).

Trichogramma brassicae—native to Europe is used to control lepidopteran vegetable pests such as European corn borer (Babendreier et al. 2003).

Trichogramma pretiosum—native to North America for lepidopteran cotton and vegetable pests (e.g. bollworms and budworms) (Pluke and Leibe 2006).

Effective integrated pest management relies on the incorporation of multiple pest control tools and tactics to reduce pest populations. In many cases, particularly highly disturbed settings like agriculture or urban landscapes, a biological control agent (predator or parasitoid) will not provide sufficient control on its own. Therefore, *Trichogramma* wasps should be used in combination with other pest control strategies (e.g., cultural and chemical practices) in pest management programs. *Trichogramma*

wasps are generally sensitive to most insecticides (e.g., lambda-cyhalothrin, bifenthrin, and indoxacarb) as well as some fungicides and herbicides (Cônsoi et al. 2010). The toxicity of these pesticides varies depending on the life stage exposed to the pesticide and the rate of application, which can have diminishing effects on the use of *Trichogramma* in IPM programs (Cônsoi et al. 2010). Therefore, adjusting pesticide use to minimize exposure of products to *Trichogramma* wasps and other natural enemies is an important component of an effective IPM program. For example, applying systemic insecticides as soil drenches or granular formulations can eliminate contact with host eggs and *Trichogramma* wasps, but provide control of plant pests feeding on the host plant tissue.

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