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Oviposition Strategies of Tachinid Parasitoids: Two *Exorista* Species as Case Studies

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ABSTRACT: Oviposition strategies and mechanisms of host selection in parasitoids may be crucial for the success of parasitization and parasitoid production. These aspects are far less known in tachinid parasitoids than in hymenopteran parasitoids. Depending on the species, parasitoid flies may adopt direct or indirect oviposition strategies. The 'direct type' females lay eggs on or, in relatively a few species, inside the host body. This review describes cues involved in host selection by tachinid parasitoids and their oviposition strategies and presents 2 case studies in more detail, focusing on *Exorista larvarum* and *Exorista japonica*. These 2 polyphagous parasitoids of Lepidoptera lay macrotype eggs directly on the host cuticle. Both species have been used as biological control agents in inoculative release against the gypsy moth *Lymantria dispar* in the Northern United States. Improved knowledge of the mechanisms involved in host selection and oviposition strategies may increase the possibility of eliciting oviposition by these tachinids on target lepidopterous hosts (and even artificial substrates), thus facilitating their rearing and ultimately making their exploitation as regulators of target insect pests more feasible and efficient.

KEYWORDS: Tachinidae, host selection, oviposition, *Exorista japonica*, *Exorista larvarum*, biological control

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Introduction

Tachinid flies represent fewer than 20% of all insect parasitoids, most of which are hymenopterans,[1] and are far less studied than their hymenopteran counterparts.[2,3] Yet, this family of Dipterans, with about 8500 species described worldwide,[4] is the largest and most important group of non-hymenopteran parasitoids.[2,5–7] Tachinids are oviparous or ovoviviparous endoparasitoids of a variety of insects, mostly phytophagous, about 70% of which are larval Lepidoptera.[8] The host range of these parasitoid flies also comprises other taxa, including the Heteroptera (nymphs and adults) and Coleoptera (larvae and adults).[9] The hosts of many species are, however, still unidentified.[6]

Tachinids play a major role in regulating phytophagous insect populations, and several species have potential to control target insect pests. Some of them have been used in classical biological control programmes against lepidopterous defoliators and sawflies, especially in the Nearctic and Neotropical regions.[6,10] For example, *Exorista larvarum* and *Exorista japonica*, which are examined in this review, are polyphagous parasitoids of Lepidoptera, and are known as antagonists of the gypsy moth *Lymantria dispar*. Since the early 1900s, they have been introduced several times against this defoliator into the Northern United States, although only *E larvarum* has established.[11] Neither has so far been used for augmentation, a biological control technique that has involved very few tachinid species.[6,10] The 2 *Exorista* species (as well as other tachinids) could be better exploited in biological control if knowledge of their biology, host-parasitoid interactions and behaviour can be increased and if their mass rearing can be optimized.[6] Oviposition strategies and factors stimulating oviposition represent a crucial aspect for both the success of parasitization and parasitoid production.[6] For this reason, available knowledge of the oviposition strategies and the mechanisms of host selection by both *Exorista* species is reviewed here as starting point for further research aimed at better exploiting their potential as biological control agents. The review is focused on these 2 case studies, but general information is given about the oviposition strategies of tachinid flies to stimulate research on other tachinid species.

Oviposition Strategies of Tachinid Parasitoids

As in other aspects of parasitism, the oviposition strategies and mechanisms of host selection are far less known in tachinid parasitoids than in hymenopteran parasitoids. But it is known that host selection by tachinids relies on chemical and physical cues.[5] Depending on species, tachinids may adopt indirect, direct, or, rarely, mixed oviposition strategies. For example, ormiine tachinids may oviposit on their hosts (direct strategy) or near them (indirect).[12]

Indirect strategies

Indirect strategies are far more common in tachinid parasitoids than in hymenopteran parasitoids. About 40% of Palaearctic tachinid species use indirect strategies.[13] In one of these modes, the females, which are usually ovoviviparous, deposit their eggs close to a host. First instars are generally of the planidium type and, in some species (eg, *Archytas marmoratus*), they must wait for a host to pass by. In other species (eg, *Lixophaga diatraeae*),

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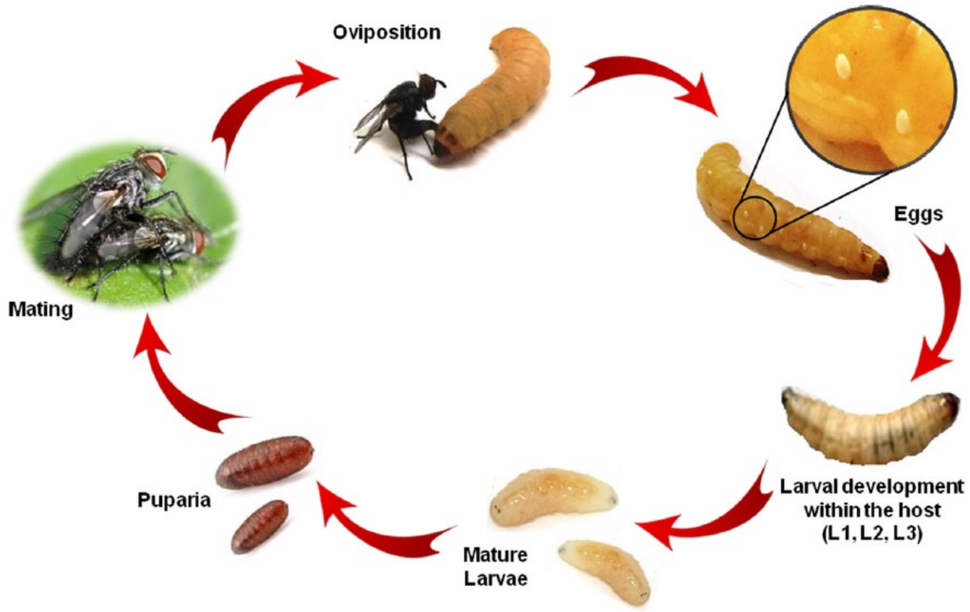

Figure 1. Scheme of the life cycle of *Exorista larvarum*.

first instars must search for a host and may thus reach victims living in concealed places that adult flies cannot reach. Most Goniini, instead, lay minute microtype eggs on the host food plant. The eggs hatch only when ingested by a host via incidental contact, without mediation by cues.[2]

In all indirect oviposition strategies, adult females use chemical and physical cues only for locating the host habitat. For example, they may be attracted to volatiles emitted by host-infested plants, thus increasing the probability that the microtype eggs will be eaten by host larvae, as seen in *Pales pavida*, a tachinid parasitoid of the noctuid species *Mythimna separata*.[14] *Pseudogonia rufifrons*, which oviposits microtype eggs on leaves, is attracted by physical cues associated with the host food plant (eg, shape, size, and leaf colour).[15] In tachinid species, which depend on first instars for host location and acceptance, the cues involved in host detection are mostly unknown. Oviposition in the host environment by *A marmoratus* was, however, stimulated by a substance isolated from larvae of *Heliothis virescens*.[16]

Any indirect oviposition strategy is associated with very high parasitoid fecundity (up to several thousand eggs) because it implies higher mortality of eggs than direct strategies.[2,3]

Direct strategies

Direct strategies represent the most common oviposition mode in tachinids.[2] Eggs may be laid on the host integument or, in some species (eg, *Carcelia gnava*), they may even be projected on the host body. More rarely (eg, *Compsilura concinnata* [17]), eggs are injected into the host haemocoel because some female sternites are used as piercing structures to perforate the host integument and guide the ovipositor into the cut. Some species, including *Rondania cucullata*, may insert eggs into the host via natural openings such as the buccal or genital-anal cavity.[18]

In the direct strategies, female flies must first locate a habitat where hosts are likely to exist and then locate hosts within this habitat. In this process, the females use long-range olfactory cues to locate the habitat (plant or other host food sources or chemicals derived from interactions between the host and the plant, such as frass).[19,20] Chemical evidence for induction of plants to attract herbivores' natural enemies, studied mainly in hymenopterans, shows that herbivore-induced plant volatiles (HIPVs) can attract parasitoids.[21] Herbivore-induced plant volatiles were found to be crucial host location cues also for the tachinids *E larvarum* and *E japonica*,[5,22,23] as explained below. Tachinids displaying direct strategies to attack pentatomids may use bug aggregation pheromones as chemical signals for host location.[20] Physical stimuli, including visual cues, also play a role in the location of habitats and hosts by tachinids using direct strategies, which have relatively large eyes.[24] Host size, colour, texture, and movements can affect the oviposition behaviour of a number of species, including *E japonica*.[6,22,25–27] Ormiine tachinids use phonotaxis for host location.[12]

So far, associative learning (the establishment through experience of an association between 2 signals or between a signal and a behavioural response [28]) has been documented in a few tachinid species, all of which use direct oviposition strategies (eg, *Drino bohemica*,[29] *Exorista mella*,[30] *Ormia ochracea*, [31] and *Exorista sorbillans* [32]). Two solitary tachinids, *Myiopharus doryphorae* and *Myiopharus aberrans*, showed the ability to recognize previously parasitized hosts, thus escaping superparasitism, but the mechanisms involved are unclear.[33]

The 2 case study insects examined in this review – *E larvarum* and *E japonica* – use a direct oviposition strategy in

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which females lay heavy-shelled, highly visible macrotype eggs on the host cuticle.[34]

Two *Exorista* Species as Case Studies of Direct Oviposition Strategies

Exorista larvarum and *E japonica* are polyphagous gregarious larval parasitoids of Lepidoptera.

Distribution, host range, and life history

Exorista larvarum is a Palaearctic species widely distributed throughout Europe, Northern Africa, and several Asian regions. About 15 lepidopterous families have been reported as its hosts.[34,35] *Exorista japonica* is found from India to East Asia, and 18 lepidopterous families are recorded as its hosts.[36] The known natural hosts for both species belong mainly to the Lymantriidae, Lasiocampidae, Noctuidae, and Arctiidae.[8,36] Both are especially known as antagonists of *L dispar*.[37]

A number of studies have described the development of *E larvarum* in the natural host *Spodoptera* (=*Prodenia*) *litura* [38] and in the factitious host *Galleria mellonella*, a pyralid moth [39,40] and of *E japonica* in the natural host *Mythimna* (=*Pseudaletia*) *separata*.[41] The newly hatched first instars of both *Exorista* species penetrate the host larval body and build primary integumental respiratory funnels, which permit them to breathe atmospheric air from the beginning of their development and thus to grow rapidly until pupation. At 26°C, the duration of *E larvarum* development from egg to pupa lasts about 8 to 9 days, and adults emerge after another 8 days.[42] The newly emerged adults mate and, after 2 to 3 days, the females lay whitish, unincubated macrotype eggs (0.5- to 0.6-mm long) on the host with their extensible ovipositor (Figure 1).[38,43]

The number of eggs laid during the female life span on host larvae is similar between the 2 *Exorista* species, and most are laid during the first 10 days.[38,40,41]

Host habitat location, host location, and host acceptance

The role of HIPVs in the location of habitats and hosts was studied intensively in *E japonica* and to a lesser extent in *E larvarum*.[5,22,23] Wind tunnel experiments showed that maize plant volatiles induced by host infestation were important cues in attracting females of *E japonica*.[22,23,44] The duration of attraction of *E japonica* to herbivore-damaged plants after the initial release of HIPVs was also studied in a wind tunnel: females continued to detect HIPVs for 24 hours after removal of larvae of the host *M separata*.[45] The extent of infestation also affected the attraction of female flies. When a maize plant was infested with 20 last instar *M separata* larvae for 1 hour and then the host larvae were removed, the rate of attraction of female flies to the plant was 70% for 5 hours but decreased gradually to 48% after 24 hours. But when a maize plant was infested with 5 host larvae for 24 hours, the rate of attraction remained at between 60% and 70% for 4 days. Moreover, the attraction to artificially damaged plants was high (85%) immediately after damage but was low (40%) at 1 hour after damage. However, uninfested leaves were not attractive when all other leaves on the same plant were infested. In addition, the uninfested parts of infested leaves were not attractive.[45]

Plant colour is an aspect of long-range orientation, as *E japonica* females use sight to locate host habitats. Females landed significantly more frequently on a green paper plant model (84.6%) than on yellow (53.8%), blue (38.5%), or red (30.8%) models when odours of host-infested plants were presented in a wind tunnel.[22]

In general, once the parasitoid females have located a potential host habitat, they stop in response to low-volatility chemicals deposited by their hosts on the substrate.[46] These short-range cues are reliable information for female parasitoids to detect the host.[47] Tachinid females use chemosensors on their front tarsi, which may function similar to those on the antennae of many hymenopteran parasitoids.[3] Infested maize leaves attract *E japonica* females also.[22,45,48,49] The females locate infested parts of the leaves [45] and extensively explore the leaf by tapping its surface with their front legs while walking. They spend significantly more time exploring infested plants than exploring artificially damaged or undamaged plants.[49] Experiments run in a wind tunnel showed that the maize plant volatiles induced by the activity of *Mythimna unipuncta* larvae were important cues to attract *E larvarum* females.[23]Chemical stimuli released by herbivore-infested plants thus play a role in attracting ovipositing *E larvarum*, as well as *E japonica* [44] and other *Exorista* species.[24]

Host frass volatiles may induce females of direct-type tachinids to stop when they enter areas in which hosts are present or likely to be present. *Exorista japonica* females stopped in response to chemicals derived from fresh frass of *M separata* larvae. [25] They clearly changed their behaviour when they touched the frass with their front tarsi: they decreased their walking speed and began intensive exploration of the frass-containing patch by tapping the frass with their legs and walking or turning within the patch.[25]

Visual cues may also be a key factor in short-range host location by direct-type tachinids. When *E japonica* females encounter a host, they turn towards it ('fixation'), walk to within 1 cm of it ('approach'), and then pursue the crawling larva on foot using visual cues to guide it.[26] Such behaviours by females in response to a moving freeze-dried larva of *M separata* and to a moving black rubber tube [27] suggest that larval movement attracts them.

Once *E japonica* has approached the host, it begins its 'examination' behaviour, which consists of facing the host and touching it with its front tarsi.[26] Sometimes, the fly moves completely around the host in one direction but often changes direction. When the host does not move, the fly stands still and faces it during an examination which can take more than

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60 minutes before attacking it.[50] In cage experiments, isolated *Spodoptera littoralis* or *G mellonella* larvae were more attractive to *E larvarum* females than *S littoralis* larvae feeding on bean leaves. As the feeding larvae were less mobile than the isolated targets, the results suggest that at close range, parasitoid females use visual cues and, in particular, motion signals, but at long range, chemical cues are more important.[51] As further proof of the importance of host movements for host location by *E larvarum*, in cage experiments, very few eggs were laid by female flies on previously killed *G mellonella* larvae (Dindo, unpublished data).

Host acceptance may be influenced by multiple factors, including physical cues. *Exorista japonica* females check the texture and curvature of the host by means of tarsal examination before oviposition. They prefer to oviposit on a cylindrical shape rather than on a flat board or a cube and on a surface with a rubbery texture than with a papery or silicone texture.[52,53]

Oviposition pattern, host defensive behaviour, and oviposition regulation

The oviposition pattern of *E larvarum* has been described in detail (Figure 1). Ovipositing females generally approach the host larva from one side, extend their ovipositor and lay eggs, mostly on the dorsal or latero-dorsal part of the host body. The eggs are attached to the host integument with the glue secreted by the female's accessory reproductive glands. They are of the dehiscent type, that is, the first instars exit the eggs by lifting up the convex upper surface and penetrate the host body in front of the egg shell.[23,8,54] Parasitization is most successful when the eggs are laid on last instar larvae, although complete parasitoid development can be achieved in younger larvae.[55]

The defensive behaviour of the larvae of 3 lepidopterous species (*G mellonella, S littoralis*, and *M unipuncta*) against oviposition by *E larvarum* has been described.[51] *Galleria mellonella* and *M unipuncta* are both factitious hosts of *E larvarum*, but only the former is well suitable to the parasitoid.[23] *Spodoptera littoralis* is a natural host of this tachinid fly.[9] The larvae of *S littoralis* and *M unipuncta* (both noctuids) react violently, wriggle, regurgitate liquids, and try to bite the ovipositing females. Often, *S littoralis* larvae turn their heads towards the egg. If they can reach it with their mandibles, they will devour it, as do other noctuid larvae following oviposition by tachinids.[2,50] *Exorista japonica* females oviposit mainly on the head and thoracic segments of the host. When one egg per host was laid on different body segments, the rate of adult emergence followed a U-shaped curve, being higher on the head, thoracic, and 10th abdominal segments and lower on the 6th and 7th segments, likely reflecting the host's ability to remove or destroy eggs laid on its body. These results suggest that *E japonica* selectively oviposits on certain parts of the host body as an adaptation to the defensive behaviour of the host.[50]

The number of eggs per host is crucial for the success of parasitization. For *E larvarum* maintained in a laboratory colony, the best results were obtained when 4 to 6 eggs were laid on *G mellonella* last instar larvae.[56] The capacity to avoid excessive superparasitism, which may lead to lower size or even death of all developing parasitoid larvae, has not been documented in *E larvarum.* In captivity, however, excessive superparasitism may be avoided by limiting the exposure of host larvae to flies.[55,56] In the field, supernumerary eggs of *Exorista* species were sometimes deposited on a single host.[57] Female *E japonica* flies, however, displayed host discriminatory behaviour when the extent of parasitism and the rate of host encounters were high: females discriminated between unparasitized and parasitized hosts (parasitized either by themselves or by other females) when 10 eggs were present on one host, but not when 5 eggs were present, which was interpreted as 'vague' host discrimination capacity.[58] Moreover, host discrimination was affected by the time interval between host exposures: females oviposited equally on an unparasitized host and a parasitized host with 10 eggs when they encountered hosts at long intervals but they laid fewer eggs on the parasitized host when the interval was short. These results suggest that the females of *E japonica* can discriminate parasitized hosts depending on the extent of parasitism and can regulate oviposition in response to host density (ie, the rate of host encounters).[58]

Out-of-host oviposition

Despite the importance of chemical and visual cues for host detection, captive *E larvarum* females usually release eggs on cage surfaces, even when host larvae are available.[38,59] This behaviour has also been reported to happen in nature.[38] As a rule, 'out-of-host' eggs are lost because the first instars cannot penetrate any host larvae. Yet, they can be retrieved for parasitoid production by placing them on an artificial medium based on skimmed milk [60] and can even compete with eggs removed from *G mellonella* larvae for in vitro rearing in terms of adult yields and parasitoid quality.[59] Therefore, the in vitro rearing of *E larvarum* may be decoupled from the availability of a living host as it may be started from 'out-of-host' eggs. Direct oviposition on artificial medium has, however, not been obtained so far. Further knowledge of the chemical and physical signals involved in oviposition by *E larvarum* is therefore necessary to enhancing oviposition on artificial substrates.

Conclusions

Tachinid flies are important biological control agents of phytophagous insect populations, but information on the oviposition strategies of these parasitoids is limited, in particular of the indirect-type species. Research on oviposition has been conducted in a scant few tachinid species, most of which, including *E larvarum* and *E japonica*, use direct strategies. These 2 species are, however, important and deserve attention because of their

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potential as biocontrol agents not only of *L dispar* and other forest defoliators but also of agricultural lepidopterous pests, such as *M unipuncta* [23] and *M separata*.[25] Both *Exorista* species are suited to mass rearing and may thus be considered good candidates for applied biological control of target lepidopterous species because the success of biological control is based largely on the availability of effective procedures for rearing the parasitoids used.[6,61] Improved knowledge of the mechanisms involved in host selection and oviposition may increase the possibility of eliciting oviposition by these 2 species on selected hosts (and even artificial substrates), thus further facilitating their rearing and ultimately making their exploitation as regulators of target insect pests more feasible and efficient.

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Author Contributions

MLD and SN jointly contributed to the development of the structure and arguments for the paper and to the writing of the manuscript. Both the authors reviewed and approved the final manuscript.

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