

Oviposition Site Selection by the Predatory Midge *Aphidoletes aphidimyza* (Diptera: Cecidomyiidae)

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ABSTRACT Eggs and neonate larvae of the aphidophagous midge *Aphidoletes aphidimyza* Rondani are vulnerable to intraguild predation and starvation. The role of *A. aphidimyza* females in selecting suitable oviposition sites for offspring survival and development was investigated in the laboratory on potato. Oviposition preference, measured as the number of eggs laid in different microhabitats, increased with density of the potato aphid, *Macrosiphum euphorbiae* (Thomas), and plant pubescence. However, midge females do not discriminate between plants colonized by the coccinellid predator *Coleomegilla maculata lengi* Timberlake and those that are not. *A. aphidimyza* egg survival in the presence of *C. maculata* larvae and adults was higher in sites characterized by a high density of trichomes than in other microhabitats. The selection of pubescent leaves infested with aphids by ovipositing females reflects both the food dependence and predation risk constraints of immature midges.

KEY WORDS aphid, aphidophagous, habitat selection, ovipositional preference, prey density, trichome

OVIPOSITION SITE SELECTION by insects is often made to balance vulnerability of eggs to natural enemies with foraging profitability of emerging larvae. Insect eggs are vulnerable to predation and parasitism and, although they cannot rely on the escape and aggressive behaviors of mobile stages, an array of morphological and chemical defensive devices have evolved (Hinton 1981). For example, eggs may be laid on stalks (Duelli and Johnson 1991), covered by excrement (Damman and Cappuccino 1991), or protected by armor or oil (Eisner et al. 1996). Furthermore, females can increase egg survival through maternal care or selection of less exposed oviposition sites (Edmunds 1974, Hinton 1981). Choosing a suitable oviposition site also ensures that emerging larvae are in close proximity to a food source. Neonate larvae are usually fragile and can be subject to desiccation and starvation.

The aphidophagous midge *Aphidoletes aphidimyza* Rondani is a specialist predator of aphids commonly used in biological control programs (Markkula and Tiittanen 1985). Females lay single or small clusters of eggs on foliage, within or close to aphid colonies (Nijveldt 1988). Ovipositing females have the capacity to discriminate among plant species, plant varieties, artificial substrates, and plants infested or not by aphids (Mansour 1976). El-Titi (1973, 1974) showed that females are able to locate a single infested *Brassica* plant among 75 noninfested plants in a greenhouse, and lay eggs according to aphid density. Such well developed discriminating capacities are crucial for *A. aphidimyza* survival, because neonate larvae will starve to death if they are >63 mm from food (Wilbert 1973). Neonate larvae, which use olfactory and visual

cues to locate aphids, could not detect prey unless it was very close to them (≈ 3 mm).

Confined within aphid colonies, *A. aphidimyza* are vulnerable to intraguild predators. Under laboratory conditions, 70–80% of *A. aphidimyza* eggs and larvae are killed by the spotted lady beetle *Coleomegilla maculata lengi* Timberlake (Coleoptera: Coccinellidae) or the lacewing *Chrysoperla rufilabris* Burmeister (Neuroptera: Chrysopidae) (Lucas et al. 1998). Interactions between the midge and the intraguild predators were asymmetric in favor of the coccinellid and the lacewing. Furthermore, intensity of intraguild predation generally decreased as the abundance of aphids increased (Lucas et al. 1998).

Selective pressure associated with requirement to rapidly find prey at short distances for neonate larvae as well as the risk of intraguild predation for eggs and larvae must have had a significant role in determining *A. aphidimyza* oviposition strategy. Oviposition site selection might, therefore, reflect a trade-off between laying eggs near an aphid colony, where intraguild predation is likely to be intense but foraging of neonate larvae more successful, and laying eggs at a distance from an aphid colony where intraguild predation would be lower but neonate larvae more susceptible to starvation.

In this study, we examine some of the factors that influence oviposition site selection by *A. aphidimyza* females. We predict that under suitable conditions of prey availability, females select protected oviposition sites in the vicinity of an aphid colony. We also expect females to avoid aphid colonies that are already exploited by other aphidophagous predators. In the lab-

oratory, we examined the effects of plant architecture, aphid density, trichome density, and intraguild predator presence on the distribution of *A. aphidimyza* eggs. Next, we determined how oviposition site selection may influence predation on *A. aphidimyza* eggs by *C. maculata*.

Materials and Methods

Potato aphids, *Macrosiphum euphorbiae* Thomas (Homoptera: Aphididae), were collected near Québec City (Canada) and maintained on potato plants, *Solanum tuberosum*, 'Norland'. *C. maculata* and *A. aphidimyza*, originally obtained from commercial suppliers, were reared on *M. euphorbiae* at $23 \pm 1^\circ\text{C}$, 60–70% RH, and a photoperiod of 16:8 (L:D) h. In all tests, 2- to 4-d-old mated *A. aphidimyza* females were used.

Oviposition Site Selection. Oviposition sites were first characterized according to plant architecture and aphid density. The experimental set-up consisted of a potato seedling, Norland, with 8 leaves placed in a cage (266 mm high by 105 mm diameter). Twenty-four hours before the test, 2 cohorts of 20 second-instar aphids were introduced on the 2nd (L2) and 5th (L5) leaves using clip-cages. At the beginning of the experiment, clip-cages were removed and 5 *A. aphidimyza* females were introduced in the cage. Three days later, the position of each *A. aphidimyza* egg and aphid was recorded and classed as being on the apex, stem, or leaves (leaf 1, leaf 2, leaf 3, . . . leaf 8) of the potato seedling. This experiment was replicated 12 times. The relationship between the number of eggs laid and aphid density was analyzed using a linear regression (Scherrer 1984).

Effect of Trichome Density. To evaluate the effect of trichome density on oviposition site selection by *A. aphidimyza*, we first examined the distribution and density of trichomes on 40–50 cm high potato seedlings bearing 11 leaves. Trichome density was measured on different parts of the plant (stem, leaf 1, leaf 2, leaf 3, . . . leaf 11, apex) and a height index was used, ranging from 1 (lowest leaf) to 12 (apex). We placed a glass ring (1.56 mm in diameter) in the middle of the leaf, adjacent to the main veins, and recorded the number and type of trichomes on both surfaces of the leaf disk (1.91 mm²) using a stereomicroscope. Type A trichomes are short with a tetralobulate gland at the tip, whereas type B are longer and without glands (Tinguey and Laubengayer 1981). Both types of trichomes were pooled in the analysis as their relative proportion remained constant among plant parts analysis of variance (ANOVA), $df = 11, 92; F = 1.103; P = 0.3679$; frequency data were analyzed using arcsine transformation). These observations were replicated 12 times. An ANOVA was used to determine the relationship between trichome density and height index.

We then determined if there was a relationship between trichome density and oviposition preference by *A. aphidimyza*. In this instance, 1 leaf with a low density of trichomes (<25 trichomes per square millimeter) was placed next to one with a high density of

trichomes (>50 trichomes per square millimeter) and was offered to ovipositing females. The 2 leaves were excised, their petiole plunged into cups filled with water, and placed side by side in a cage (26 by 36 by 37 cm). Leaves were of similar size, held at the same height, and infested by 16 second-instar aphids. Five *A. aphidimyza* females were introduced in the cage at the beginning of the test. Three days later, the number of aphids and *A. aphidimyza* eggs were recorded on each leaf using a stereomicroscope. Eight replicates were done. Paired *t*-tests were used to compare the number of eggs and aphids on both leaves (Scherrer 1984).

Effect of Predator Presence. We determined if *A. aphidimyza* females have the capacity to detect the presence of a coccinellid predator on a plant and avoid laying eggs. Two potato seedlings (10 cm high) bearing 4 leaves were placed 50 mm apart in a cage (26 by 36 by 37 cm). A colony of 30 second-instar aphids was settled on the 3rd leaf as previously described. For treatments with live predators, 40 aphids were used to compensate for predation and aphids preyed upon were renewed daily. In all experiments, a predator-free seedling was tested against one with *C. maculata*. The following 4 coccinellid treatments were conducted: (1) 2 dead adults, (2) 2 live adults, (3) 4 dead 1st instars, and (4) 4 live 1st instars. These treatments allowed us to evaluate the effect of movement and aposematic elytral pattern of adult coccinellids on the oviposition pattern of *A. aphidimyza*. The posterior wings of live coccinellids were cut before the experiment to prevent flying and pots were covered with flunon to prevent the insect from climbing. All live coccinellids survived to the end of the experiment. Dead predators were glued (Lepage bondfast) on the upper and lower surface of the 3rd or 4th leaf. Four *A. aphidimyza* females were introduced in the cage at the beginning of the test. After 72 h, the number of eggs laid on each plant was recorded. Thirteen replicates were conducted per treatment. Paired *t*-tests were used to compare the number of eggs laid on plants with predators and those without (Scherrer 1984).

Susceptibility of *A. aphidimyza* Eggs to Predation. We examined, in the absence of aphids, the influence of egg distribution and trichome density on the susceptibility of *A. aphidimyza* eggs to predation by *C. maculata*. In the 1st experiment, a loose batch of 5 one-day-old eggs was placed in 10 locations on a potato seedling: stem, petiole, and upper and lower surfaces of the edge, leaflet, central vein, and center of the leaf. Tests were started by introducing 1 coccinellid, starved for 24 h, at the base of the stem. Predator treatments consisted of *C. maculata* 1st- and 4th-instar larvae and adults. Egg mortality was recorded after 24 h. Ten to 11 replicates were conducted for each treatment and predators were used only once. Survival of eggs among sites was compared using *G*-tests (likelihood ratio).

To determine the effect of trichome density on egg survival, 2 foliar disks (9 mm in diameter) with low trichome density (<50 type B trichomes) and 2 foliar disks with high trichome density (>80 type B

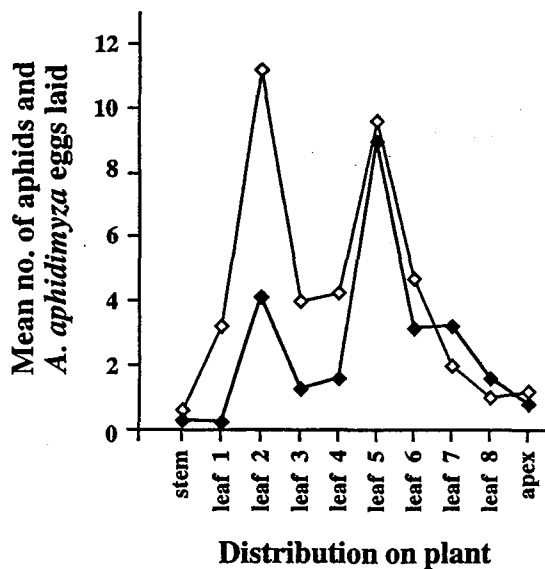


Fig. 1. Distribution of *A. aphidimyza* eggs (◆) and *M. euphorbiae* 2nd instars (◊) on potato seedlings. Data from lower and upper leaf surfaces were pooled.

trichomes) were deposited randomly upside down on agar in a petri dish (80 by 15 mm). A batch of 10 *A. aphidimyza* eggs was placed in the center of each disk. Tests started with the introduction of a coccinellid predator between the leaf disks and lasted for 2 h. Three stages of the predator were tested: 1st- and 4th-instar larvae and adult. Eggs were examined immediately after the test and evidence of predation was assessed under a stereomicroscope. Eleven replicates were done for each treatment and predators were used only once. Egg survival, under conditions of low or high trichome density, was compared using paired *t*-tests (Scherrer 1984).

Results

Oviposition Site Selection. Four hundred and ninety-two of the 499 *A. aphidimyza* eggs were laid on the undersurface of the leaves (98.6%), singly (18.8%), in compact masses (12.6%), or in loose batches (68.6%). All parts of the potato plant were used for oviposition, but very few eggs (1.2%) were found on the stem (Fig. 1). There was a significant, positive relationship between the number of eggs laid and aphid density ($F = 5.58$; $df = 1, 138$; $P = 0.02$; $R^2 = 0.04$). However, the relationship was less obvious on the lower part of the plant (leaves 1-4) (Fig. 1).

Effect of Trichome Density. Trichome density ranged from 2.62 to 16.58 trichomes per square millimeter on the upper leaf surface, and from 12.30 to 85.34 trichomes per square millimeter on the lower leaf surface. Trichome density increased from the bottom of the plant to the top (ANOVA, $F = 20.39$; $df = 11, 92$; $P < 0.0001$) (Fig. 2), to a maximum density of 100.21 trichomes per square millimeter in the apex. Stems were glabrous.

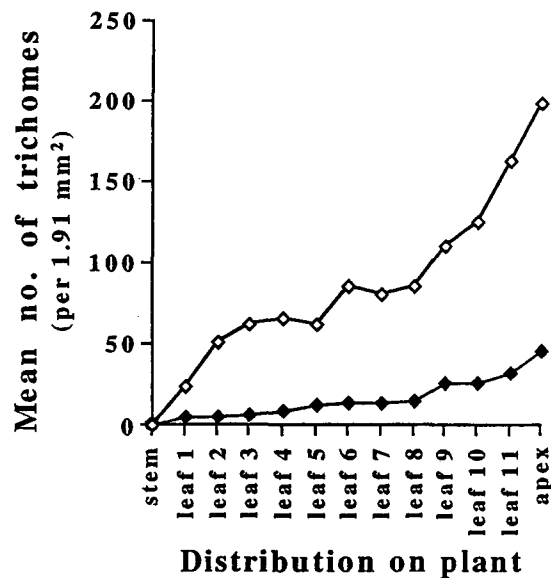


Fig. 2. Density of trichomes on the upper (◆) and lower surfaces (◊) of leaves, apex, and the stem of potato seedlings.

Females of *A. aphidimyza* laid 25.8 ± 7.4 (mean \pm SE) eggs on leaves with high trichome density compared with 12.3 ± 4.7 eggs on leaves with low trichome density ($t = -2.44$, $df = 7$, $P = 0.045$). The number of aphids recovered averaged 14.4 ± 1.3 on leaves with high trichome density compared with 15.4 ± 1.6 on leaves with low trichome density ($t = -0.40$, $df = 7$, $P = 0.7035$), suggesting that aphid density did not influence oviposition site selection.

Effect of Predator Presence. The presence of coccinellid did not affect choice of oviposition site by *A. aphidimyza* (Fig. 3). The number of eggs laid was similar on predator-free plants to that of plants with live adults ($T = -0.73$, $df = 12$, $P = 0.477$), dead adults ($T = -1.34$, $df = 12$, $P = 0.205$), live larvae ($T = 1.65$, $df = 12$, $P = 0.124$), and dead larvae ($T = 1.12$, $df = 12$, $P = 0.285$).

Susceptibility of *A. aphidimyza* Eggs to Predation. Survival of *A. aphidimyza* eggs differed significantly according to oviposition sites in the presence of 4th instar ($G_9 = 68.04$, $P = 0.0001$; Fig. 4B) and adult coccinellids ($G_9 = 73.28$, $P = 0.0001$; Fig. 4C), whereas there was no significant difference with 1st instars ($G_9 = 15.44$, $P = 0.09$; Fig. 4A). The incidence of predation was highest on the stem for 4th instar ($G_1 = 4.03$, $P = 0.045$) and adult coccinellids ($G_1 = 5.04$, $P = 0.03$).

In petri dishes, coccinellids ate more eggs on leaf disks with low trichome density than on disks with high trichome density (1st instar, $T = -2.01$, $df = 10$, $P = 0.036$; 4th instar, $T = -3.79$, $df = 10$, $P = 0.002$; adult, $T = -4.77$, $df = 9$, $P = 0.001$; Fig. 5).

Discussion

This study emphasizes the role of *A. aphidimyza* females in providing both food and protection to im-

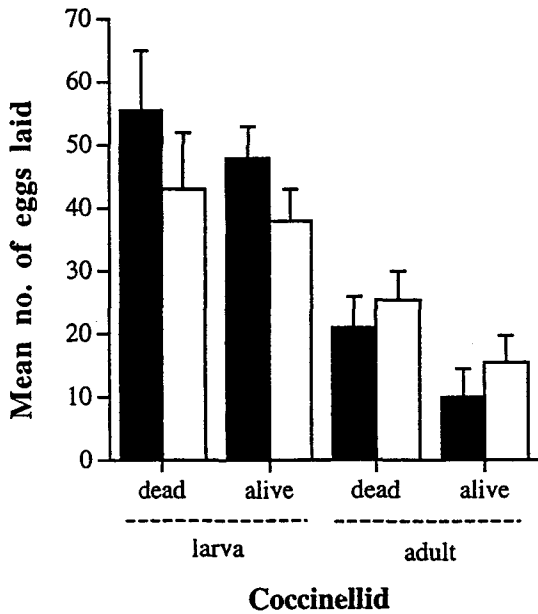


Fig. 3. Number of eggs (mean \pm SE) laid by *A. aphidimyza* females on potato seedlings with (open bars) or without (solid bars) *C. maculata* larvae or adults. No significant differences were found between treatments (*t*-test, $P > 0.05$).

mature midges. Ovipositing females face the apparent trade-off between foraging profitability of emerging larvae and vulnerability to intraguild predators by selecting pubescent leaves infested with aphids.

Our results are similar to those of El-Titi (1972/1973), where the number of eggs laid by *A. aphidimyza* increased as a function of aphid density. Selective pressures, other than those to enhance feeding opportunities of neonate larvae, may have had a significant role in shaping the preference of *A. aphidimyza* to lay eggs within an aphid colony. Aphids typically form large aggregations that often attract an array of natural enemies. Within aphidophagous guilds, *A. aphidimyza* eggs and larvae are highly vulnerable to intraguild predation (Lucas et al. 1998). However, *A. aphidimyza* may benefit from a dilution effect within an aphid colony that reduces the incidence of intraguild predation (unpublished data). The dilution effect decreases the individual's probability of being attacked once the prey colony has been detected by natural enemies (Taylor 1977, Inman and Krebs 1987). Thus, females ovipositing within aphid colonies not only provide food to neonate larvae, but also protect them against intraguild predators.

Trichomes constitute outgrowths of the epidermis of leaves, shoots, or roots that affect, mechanically or chemically, insect feeding, locomotion, attachment to the plant, and oviposition (Norris and Kogan 1980). In several systems, plant pubescence has been shown to either increase or reduce oviposition in both phytophagous and predaceous insects. For example, whiteflies (Homoptera: Aleyrodidae) laid significantly

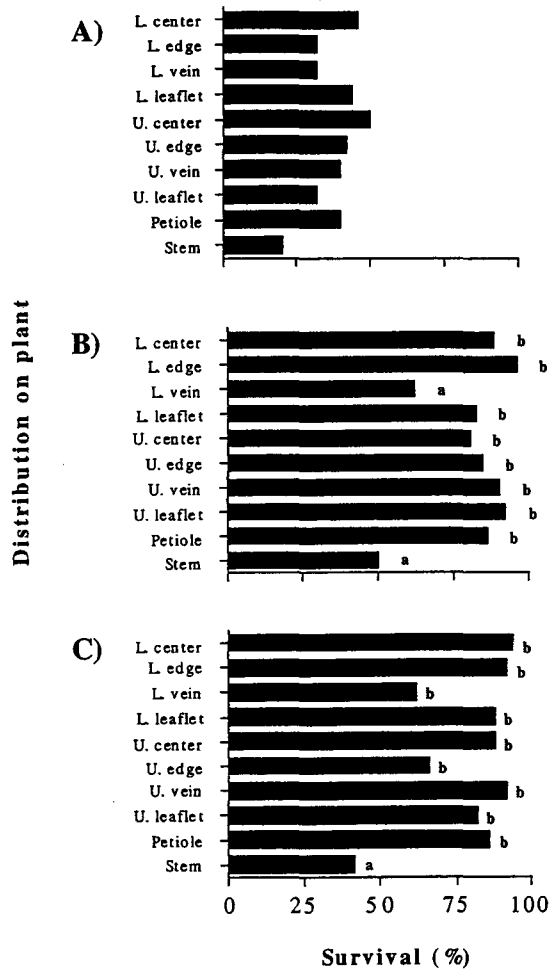


Fig. 4. Percent survival of *A. aphidimyza* eggs according to their distribution on potato seedlings when exposed to *C. maculata* 1st instar (A), 4th instar (B), and adults (C). Percentages followed by different letters are significantly different (*G*-test, $P < 0.05$). U, upper leaf surface; L, lower leaf surface.

more eggs on hirsute and pubescent cultivars of soybean and cotton than on glabrous ones (Butler et al. 1986, McAuslane 1996). However, the number of eggs laid by cereal leaf beetles (Coleoptera: Chrysomelidae) on wheat (Norris and Kogan 1980), and by predatory lacewings (Neuroptera: Chrysopidae) on potatoes (Obrycki and Tauber 1984) was reduced with an increase in leaf trichome density.

In this study, *A. aphidimyza* females prefer to lay eggs in sites with high trichome density where predation by coccinellids is reduced. Obrycki and Tauber (1985) observed that adult coccinellids were distributed evenly among potato cultivars with different pubescence, but eggs were more abundant on plants with high trichome density, suggesting a higher level of egg predation on less pubescent plants. A few studies have described how plant pubescence may interfere with the foraging behavior of aphidophagous coccinellid

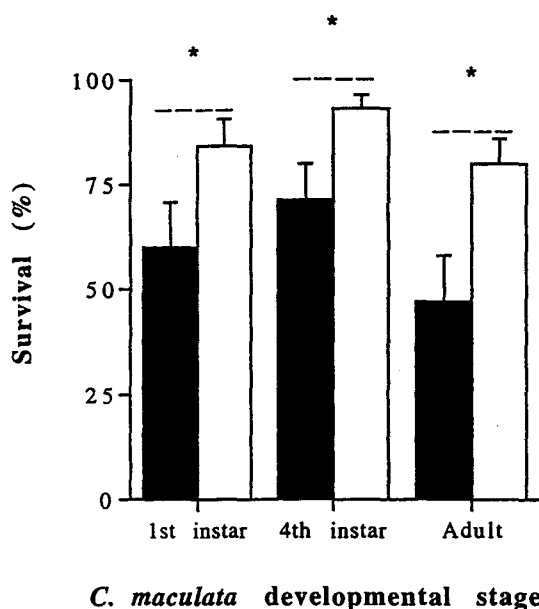


Fig. 5. Percent survival of *A. aphidimyza* eggs at low (solid bars) and high (open bars) trichome densities when exposed to various developmental stages of *C. maculata*. For each type of predator, percentages followed by different letters are significantly different (G -test, $P < 0.05$).

(*C. maculata*, *Adalia bipunctata*, *Coccinella septempunctata*, *Coccinella transversoguttata*, and *Hippodamia convergens*), chrysopid and syrphid larvae (Norris and Kogan 1980, Obyrcki and Tauber 1984, Hodek and Honék 1996). As shown for *H. convergens* on tobacco, a high density of trichomes reduced the searching speed of larvae on plants (Elsy 1974) and increased their probability of being captured by glandular trichomes (Belcher and Thurston 1982). Similarly, glandular trichomes increase *C. maculata* larval mortality and reduce *Helicoverpa zea* (Boddie) egg consumption on tomatoes (Barbour et al. 1993). However, trichomes should not constitute a major mechanical obstacle to cecidomyid movement. Midge larvae are maggot-like and small, with neonate larvae measuring 0.3 mm and fully-grown larvae ≈ 2.5 by 0.7 mm. They are then better adapted to move between trichomes than large campodeiform coccinellid larvae. Of particular significance is the observation that small, 1st-instar *C. maculata* were more efficient in capturing eggs of *A. aphidimyza* than large, 4th-instar coccinellids.

In addition to diminishing predator locomotive capability, trichomes may operate as a physical barrier to predators by preventing egg detection and capture on plant substrate. Several aphidophagous species use tactile cues to find their prey (Canard and Duelli 1984, Majerus 1994) and small eggs stuck within a tangle of trichomes may be difficult to locate.

There might be another advantage for ovipositing *A. aphidimyza* females to prefer aphid-infested sites with high trichome density. These sites usually correspond

to younger leaves (the density of trichomes on potato decreases as leaves expand) and, thereby, to microhabitats that are often the most suitable for *M. euphorbiae* development (Boiteau 1997). Therefore, midge females might associate trichome density to the ongoing and future quality of the microhabitat for their offspring. This strategy, called "buy-futures," was first proposed by Kan (1988) who observed that aphidophagous hoverflies (Diptera: Syrphidae) prefer to lay their eggs in young aphid colonies consisting of nymphs or fundatrices than in degenerating colonies. Thus, factors associated with antipredator defense, as well as the quality of the microhabitat may work together to make young pubescent leaves the most suitable oviposition sites for *A. aphidimyza*. However, this hypothesis might not hold true for *Myzus persicae* (Sulzer), which is another aphid species that prefers to colonize senescent potato leaves (Boiteau 1997).

The degree to which predation risk is involved in shaping *A. aphidimyza* ovipositional decisions is not fully understood. We expected females to have evolved discriminating capacities that enable them to detect the presence of intraguild predators on potential oviposition sites. However, we were unable to demonstrate any avoidance for plants colonized by coccinellids predators. Three nonexclusive reasons might be involved. First, *A. aphidimyza* females are not able to detect aphidophagous predators, which form a very diverse guild, or gauge the likelihood of attack on their offspring. Second, the 'aphid stimulus' is sufficiently strong to negate the perception of danger by females and favor the completion of the oviposition sequence. This argument does not preclude the selection of protected sites near the aphid colony. Third, midge eggs are not costly to produce, and females increase the probability that at least 1 egg will survive by ovipositing even in high predation risk situations.

Our results, together with the findings of El-Titi (1972/1973), Wilbert (1973), and Mansour (1976) attest to the distinct and acute discriminating capacities of foraging *A. aphidimyza* females. Further work is required on the mechanisms of prey location, assessment of aphid and trichome densities, and egg laying behavior to better understand the observed oviposition strategy.

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