PLANT ANIMAL INTERACTIONS

E. L. Zvereva · N. E. Rank

Fly parasitoid *Megaselia opacicornis* uses defensive secretions of the leaf beetle *Chrysomela lapponica* to locate its host

Abstract Larvae of the leaf beetle *Chrysomela lapponica* derive a defensive secretion from salicyl glucosides found in the host plant *Salix borealis*. This secretion protects beetle larvae from some natural enemies, but does not appear to repel parasitoids. We tested the hypothesis that the fly parasitoid *Megaselia opacicornis* (Diptera, Phoridae) uses the larval defensive secretion of *Ch. lapponica* in its search for prey. In the field, nearly 30 times more *M. opacicornis* individuals were caught on leaves coated with sticky resin next to a source of secretion than on control leaves. In the laboratory, *M. opacicornis* females laid six times more eggs next to a cotton ball soaked in secretion than next to one soaked in water. Fly females also lay more eggs on prey rich in larval secretion than on secretion-poor prey. In the field, removal of defensive secretion from beetle prepupae resulted in a 7.5-fold reduction of oviposition by fly females. Parasitoids were nearly twice as likely to lay eggs on prepupae, rich in secretion, as on pupae, which contain little secretion. Fly offspring reared from beetle prepupae reached a 21% larger body mass than those reared from pupae. Finally, *M. opacicornis* females avoided host prepupae already parasitized by the tachinid fly *Cleonice nitidiuscula*, which possess little secretion. These experiments indicate that host plant-derived defensive secretions are used by this parasitoid for host location. Adaptation of parasitoids to use defensive secretions of hosts may selectively favor an increase in diet breadth in specialist herbivores.

Keywords Three trophic-level interactions · Oviposition · Host selection behavior · Kairomone · Olfactory attractant

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Introduction

Insect predators and parasitoids overcome substantial obstacles to locate and select high-quality prey as a nutritional source for their offspring. These obstacles appear all the more formidable when one considers the small body size of most insects, natural environmental heterogeneity, and the distances that separate potential prey populations. Many natural enemies of insect herbivores use chemical cues, such as plant volatiles and herbivore-emitted compounds, to search for prey (Turlings et al. 1990; Vet and Dicke 1992; Paré et al. 1999). Chemicals emitted by prey, but used by natural enemies for their own benefit, are called kairomones (Brown et al. 1970; Dicke and Sabelis 1988). Natural enemies have evolved to use a wide variety of natural products as kairomones, including feces, exuviae, glandular secretions, interspecific pheromones, and honeydew (Vet and Dicke 1992; Sengonca and Liu 1994). However, we are aware of only two studies that document that a prey defensive secretion acts as a kairomone. Mattiacci et al. (1993) showed that the egg parasitoid *Trissolcus basalis* (Woll.) is attracted to a chemical isolated from defensive secretion of the bug *Nezara viridula* (L.). Larval defensive secretions of some chrysomelid beetles attract and stimulate feeding by larvae of predatory syrphid flies in the genus *Parasyrphus* (Rank et al. 1996, 1998; Köpf et al. 1997; Gross 2001).

Larvae of the leaf beetle *Chrysomela lapponica* L. derive a defensive secretion, which consists mostly of salicylaldehyde, from salicyl glucosides (SGs) in the host plant (Hilker and Schulz 1994; Schulz et al. 1997). Beetles feeding on SG-poor hosts produce little defensive secretion and it does not contain salicylaldehyde (Gross and Hilker 1995). The pupal parasitoid *Megaselia opacicornis* Schmitz (Diptera, Phoridae) causes up to 40% mortality in natural populations of *Ch. lapponica* in NW Russia and Finnish Lapland (Zvereva and Kozlov 2000; Zvereva and Rank 2003). Parasitism by *M. opacicornis* is spatially density dependent, which suggests that this parasitoid may use chemical cues to locate prey from a distance (Zvereva

and Kozlov 2000). In addition, Zvereva and Rank (2003) recently demonstrated that *M. opacicornis* parasitism and oviposition was greater on beetles on SG-rich host species than on beetles on SG-poor species (Zvereva and Rank 2003). These results indicate that the beetle's defensive secretion attracts *M. opacicornis* for prey location and oviposition.

The aim of the present study was to test the hypothesis that the defensive secretion of *Ch. lapponica* larvae functions as a kairomone that attracts the phorid parasitoid *M. opacicornis*. We also determined whether parasitoid choice of prey rich in defensive secretion enhances the performance of *M. opacicornis* offspring. We addressed three questions.

1. First, we established whether adult flies were attracted to a source of beetle secretion in nature by placing a source of secretion next to a sticky resin and counting the number of flies adhering to the resin.
2. Second, we conducted laboratory and field choice tests to determine whether fly females prefer to oviposition prey types with more secretion over those that produce less secretion.
3. Third, we compared survival and body mass of parasitoids reared from different prey types. Because the prey types differ in their amount of secretion, these comparisons addressed fitness consequences for the parasitoid of using the prey secretion as an attractant and oviposition cue.

Materials and methods

Study area and organisms

The study was conducted in secondary growth habitats dominated by willow and birch, where *Ch. lapponica* was especially abundant, near the city of Monchegorsk in Kola Peninsula, NW Russia, (Zvereva et al. 1995a, 1997b). *Chrysomela lapponica* feeds on several naturally occurring willow species in this area, but clearly prefers *Salix borealis* (Fries.) Nasar. (= *Salix myrsinifolia* subsp *borealis*) over other willows (Zvereva et al. 1995b). *Salix borealis* contains very high concentrations of SGs (Tahvanainen et al. 1985; Julkunen-Tiitto 1989). *Chrysomela lapponica* females lay one to seven batches of 30–40 eggs (Zvereva et al. 1995b). After larvae hatch, they feed in groups until they disperse during the third instar. When disturbed, larvae release droplets of defensive secretion from eversible glands on the dorsal side of the thorax and abdomen. At the end of larval development, third-instar larvae attach to the upper side of leaves by the tip of the abdomen for 2 days before pupation. Defensive glands still contain substantial amounts of secretion during this immobile stage, called prepupa.

Two parasitoids cause up to 80% total mortality on beetle immature stages in the study region (Zvereva et al. 1995b, 1997a; Richter and Zvereva 1996; Zvereva and Kozlov 2000). The tachnid fly *Cleonice nitidiuscula* (body length 5 mm) attacks beetles during the early larval stage. One *Cl. nitidiuscula* larva develops in a beetle, which reaches the prepupal stage before the parasitoid completes development. Parasitized beetles exhibit reduced defensive twitching and production of secretion compared to unparasitized individuals.

The second parasitoid, *M. opacicornis* (2–3 mm), is a scuttle fly (Phoridae) that attacks leaf beetle prepupae and occasionally pupae. To oviposit, a *M. opacicornis* female sits on the leaf and extends its ovipositor towards the beetle. Eggs are laid on the prepupa where it is attached to the leaf or on the leaf up to 1 cm away from the beetle. When disturbed by *M. opacicornis*, a beetle prepupa twitches rapidly and releases droplets of defensive secretion (Kanervo 1946; Zvereva and Rank 2003). *Megaselia opacicornis* flies occasionally lay eggs on host prepupae parasitized by *Cl. nitidiuscula* (Zvereva and Rank 2003).

Attractiveness of pure larval defensive secretion to *M. opacicornis* in nature

To establish whether the larval defensive secretion of *Ch. lapponica* attracts *M. opacicornis*, we compared the number of flies that landed on a sticky resin near a source of beetle secretion to the number found on sticky resin near a control solution. These experiments were conducted in the field in late July 2003, when most *Ch. lapponica* individuals had reached the third instar, which is the final instar before pupation. We haphazardly selected three branches on each of ten *S. borealis* plants at a site where *Ch. lapponica* is abundant. On each branch, we coated two leaves of equal size, about 10 cm apart, with a sticky resin (Pestifix, Flora, Tallinn). We then placed a moist cotton ball that had been treated with secretion (treatment) or water (control) onto the center of the resin coating and counted the number of *M. opacicornis* adults stuck to the resin after 30 min. To apply larval secretion, we moistened the cotton ball and rubbed it gently against three to five third-instar *Ch. lapponica* larvae until they released droplets from their secretion glands. To analyze these data, we first obtained plant means for the number of flies found on the sticky resin surrounding treatment and control branches, and used non-parametric Wilcoxon signed-ranks tests to compare mean number of flies per treatment per plant. We used the non-parametric test because no flies were found on resin in some branches, yielding a high proportion of zeroes.

Effect of secretion on host attractiveness for *M. opacicornis*

Laboratory oviposition tests

To determine whether *M. opacicornis* females are attracted to oviposit on a source of secretion, we conducted laboratory choice tests, using methods described in Zvereva and Rank (2003). We collected *M. opacicornis* flies by an aspirator, placed 10–20 individuals in 1-l glass jars, and tested oviposition preference in two to five trials per jar ($n=5$ jars). The variation in the number of *M. opacicornis* was high because flies do not survive long and we wanted to make sure that enough flies were present to detect differences in oviposition behavior. The variation in fly number per jar contributed to the final variation in number of eggs laid.

Trials were stopped after 2–4 h, after multiple *M. opacicornis* eggs had been laid on or near a potential host item. Jars were cleaned and host items replaced between trials.

For each experiment, we exposed two host items that differed in amount of defensive secretion to ovipositing females. In the first experiment, we offered beetle pupal skins that had been placed on a moist cotton ball and counted the number of *M. opacicornis* eggs laid on or near the pupal skin. One pupal skin was placed on a source of secretion and the other on a control. We applied larval secretion to the test cotton ball by disturbing a third-instar beetle larva until secretion was released. To eliminate previous odors, each pupal skin was heated in an oven for 2 h at 200°C prior to the experiment. This experiment was conducted to measure fly egg-laying behavior, rather than simply attraction to a potential food source or oviposition site.

In the second experiment, we offered *M. opacicornis* females a choice between beetle prepupae whose secretion had been removed and undisturbed prepupae with intact secretion. We removed secretion by absorbing it onto a piece of filter paper while disturbing prepupae. In the third experiment, we offered *M. opacicornis* females a choice between a beetle prepupa and a pupa. Larval defensive glands are active in prepupae (Zvereva and Rank 2003),

but the only source of defensive secretion in a pupa is found in the skin of the third larval instar surrounding the tip of the abdomen (Pasteels et al. 1988). In the final experiment, we compared fly egg-laying rates on a prepupa that had been parasitized by the tachinid fly *Cl. nitidiuscula* versus one that was not parasitized by the tachinid. Prepupae that have been parasitized by the tachinid fly produce little secretion. To analyze these results, we obtained "jar" means for the number of eggs on each host type and conducted one-tailed paired-comparisons *t*-tests to determine whether *M. opacicornis* females had laid more eggs on secretion-rich host types than on secretion-poor ones.

Secretion removal experiment in the field

To determine whether the amount of secretion affects *M. opacicornis* egg-laying rates in the field, in late July 2002 we conducted a secretion removal experiment on five haphazardly chosen *S. borealis* plants. We selected two branches per plant, removed naturally occurring herbivores, and added sticky resin to the base of the branch to prevent emigration of experimental larvae. We then placed ten field-collected third-instar larvae onto each branch for 6 days until pupation. On one branch, secretion was removed once a day, and on another larvae were left untreated. To remove secretion, we absorbed it onto a piece of filter paper once each day. At the end of the experiment, we collected beetle prepupae (*n*=64 individuals) and counted the number of *M. opacicornis* eggs laid onto or near them.

To analyze this experiment, we calculated the proportion of *Ch. lapponica* prepupae that possessed *M. opacicornis* eggs on each branch and mean number of *M. opacicornis* eggs per branch. Because *Cl. nitidiuscula* was abundant at this site, we recorded whether a beetle pupa had also been parasitized by *Cl. nitidiuscula*. We conducted an analysis of covariance of the proportion of pupae attacked and the log-transformed number of *M. opacicornis* eggs, with host plant and secretion removal treatment as grouping factors and proportion of beetle prepupae that had been attacked by *Cl. nitidiuscula* as a covariate.

Megaselia opacicornis oviposition on beetle larvae parasitized by Cl. nitidiuscula

To determine whether parasitism by *Cl. nitidiuscula* is associated with reduced oviposition by *M. opacicornis* in the field, we collected naturally occurring prepupae from ten *S. borealis* plants (*n*=270 individuals), determined whether they had been parasitized by *Cl. nitidiuscula* and counted the number of *M. opacicornis* eggs on each prepupa under a dissecting microscope. To compare *M. opacicornis* oviposition rates on prepupae with or without a *Cl. nitidiuscula* parasitoid, we calculated plant means, subtracted *M. opacicornis* oviposition rates on the tachinid-parasitized prepupae from those on unparasitized prepupae, and conducted Wilcoxon signed-ranks tests on the differences.

Megaselia opacicornis performance on different host types

We determined whether *M. opacicornis* performance depends on whether the parasitoid develops in a beetle prepupa or a beetle pupa and measured the effect of previous parasitism by *Cl. nitidiuscula* on survival and performance of *M. opacicornis*. To parasitize *Ch. lapponica* in the laboratory experimentally, we placed a single *M. opacicornis* egg onto each beetle prepupa at the point of attachment to the leaf and kept parasitized insects in vials individually. When parasitoids pupated (5–7 days), we assessed whether *M. opacicornis*, the beetle, or neither survived. We also measured pupal mass (to the nearest milligram) for *M. opacicornis* individuals that completed development, using an analytical balance (AB104, Mettler Toledo). To analyze body mass, we used one-way ANOVA to compare pupal mass of *M. opacicornis* that had developed in a beetle prepupa versus a pupa. We analyzed *M. opacicornis* survival data using contingency table analysis. In all experiments, we report the mean and standard error unless otherwise indicated.

Results

Attractiveness of pure larval defensive secretion to M. opacicornis in nature

Within the 30-min trial period, the cotton balls soaked in defensive secretion of *Ch. lapponica* larvae attracted many (up to 18, mean=3.77±0.99) adults of *M. opacicornis*, while control cotton balls were almost ignored by parasitoids (mean=0.13±0.11, Wilcoxon signed-ranks test, *n*=10, *t*=27.5, *P*=0.002).

Effect of secretion on host attractiveness for M. opacicornis

Laboratory oviposition tests

Megaselia opacicornis females generally lay more eggs on hosts that possessed a large amount of defensive secretion over those that possessed little secretion (Fig. 1). Six times more eggs were oviposited on the pupal skin that was on a source of secretion than on the control pupal skin (Fig. 1a, *t*=5.24, *n*=5, *P*=0.0032). Removing secretion from pre-pupae reduced the number of eggs by 20% (Fig. 1b, *t*=2.13, *n*=5, *P*=0.05). Flies were nearly twice as likely to lay eggs on prepupae as on pupae (Fig. 1c, *t*=2.74, *n*=7, *P*=0.017). Finally, *M. opacicornis* females tended to avoid laying eggs near beetles that had been parasitized by the tachinid fly *Cl. nitidiuscula* (Fig. 1d, *t*=1.1, *n*=5, *P*>0.15).

Secretion removal experiment in the field

In the field experiment, prepupae whose secretion had been removed experienced 7.5-fold reduced egg laying by *M. opacicornis* females compared to control prepupae (Fig. 2a, Table 1) and the mean log-transformed number of *M. opacicornis* eggs per prepupa was 18.5-fold lower in the secretion removal treatment than in the control (Fig. 2b, Table 1). On a per plant basis, the proportion of prepupae with *M. opacicornis* eggs and the log-transformed number of eggs per prepupa declined with increasing parasitism by the tachinid fly *Cl. nitidiuscula* (Table 1).
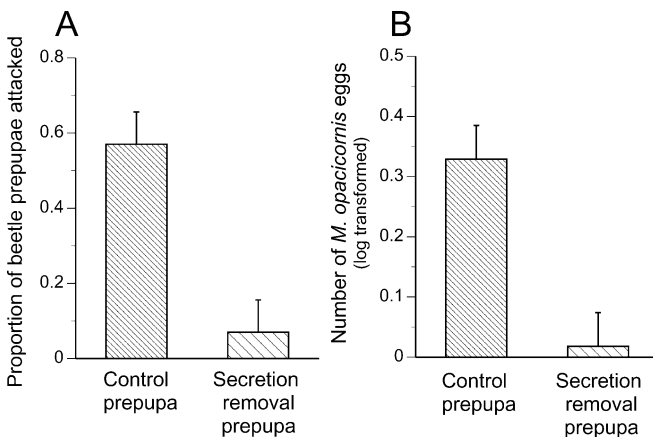
Megaselia opacicornis oviposition on beetle larvae parasitized by Cl. nitidiuscula

Of the 270 beetle prepupae collected on ten *S. borealis* clones, 85 were parasitized by *M. opacicornis*, 81 by *Cl. nitidiuscula*, and both flies parasitized 18 prepupae.
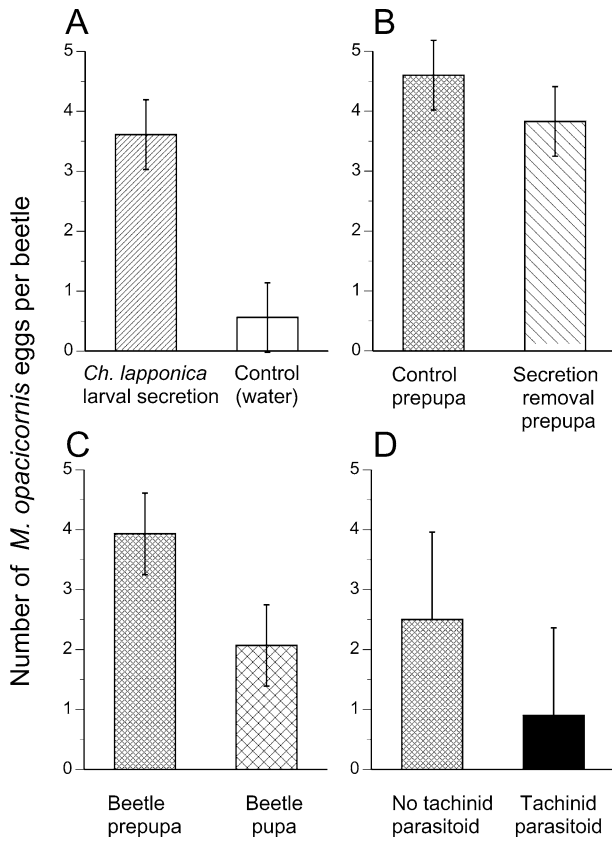
Fig. 1a–d Number of eggs laid by parasitoid *Megaselia opacicornis* on hosts with high and low amount of larval defensive secretion in the laboratory choice test. **a** Cotton ball soaked with secretion versus cotton ball soaked with water, **b** normal prepupa versus prepupa whose secretion was removed, **c** prepupa versus pupa, **d** normal prepupa versus prepupa parasitized by tachinid parasitoid *Cleonice nitidiuscula*. Data shown represent means of 2–5 trials conducted per replicate jar (*n*=5 jars) and the standard error of the difference variable used in the statistical test
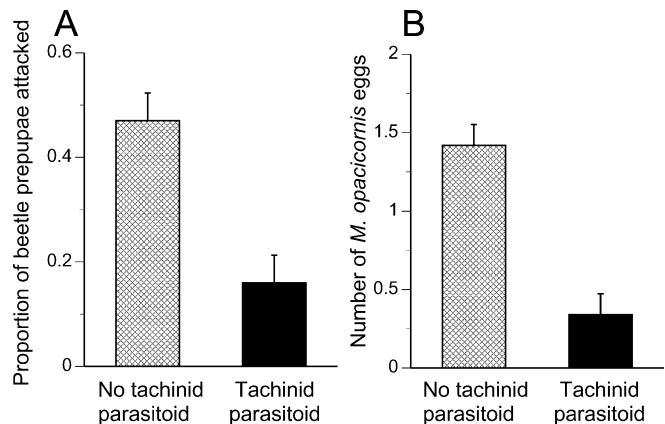
Table 1 Analysis of covariance of proportion of beetle prepupae and log-transformed number of *Megaselia opacicornis* eggs per beetle prepupa in the field secretion removal experiment

Effect	df	SS	F	P
Proportion of hosts with *M. opacicornis* eggs				
Host plant	4	0.3099	2.5	0.237
Secretion removal treatment	1	0.4382	14.2	0.033
Parasitism by *Cl. nitidiuscula*	1	0.2773	9.0	0.058
Error	3	0.0924		
Number of *M. opacicornis* eggs per host				
Host plant	4	0.0842	1.6	0.360
Secretion removal treatment	1	0.1720	13.2	0.036
Parasitism by *Cl. nitidiuscula*	1	0.1339	10.3	0.049
Error	3	0.0392		

Parasitism by *Cl. nitidiuscula* caused a 2.9-fold reduction in the likelihood of oviposition by *M. opacicornis* (Fig. 3a, Wilcoxon signed-ranks test, *n*=10, *t*=27.5, *P*=0.002). Four times more *M. opacicornis* eggs were laid on prepupae that had not been parasitized by *Cl. nitidiuscula* than on prepupae that had already been parasitized (Fig. 3b, Wilcoxon signed-ranks test, *n*=10, *t*=27.5, *P*=0.002). No *M. opacicornis* survived in 18 *Ch. lapponica* individuals that had been parasitized by *Cl. nitidiuscula*.

Megaselia opacicornis performance on different host types

Most beetle pupae that had been parasitized experimentally by *M. opacicornis* died, but 17% of them survived until adulthood. Seventy percent of *M. opacicornis* larvae that had developed in a prepupa survived (47 of 67 sampled), compared to 60% in a pupa (21 of 35 sampled, Fisher's Exact Test, *P*>0.2). Mass of *M. opacicornis* pupae was 21% greater when they had developed in a beetle

Fig. 2 *Megaselia opacicornis* parasitism rate (**a**) and log-tranformed number of eggs (**b**) laid on beetle prepupae whose secretion had been removed versus control prepupae. For each plant (*n* = 5 willows), one branch of ten control prepupae and ten prepupae whose secretion was removed were used. Data shown are least-squares means and standard errors from ANCOVA, with frequency of parasitism by *Cl. nitidiuscula* at the branch level as a covariate

Fig. 3 Field *M. opacicornis* parasitism rate (**a**) and number of eggs (**b**) laid on beetle prepupae that had or had not previously experienced parasitism by *Cl. nitidiuscula*. For each plant (*n*=10 willows), 18–71 beetle prepupae were examined for parasitism by both parasitoids (totaling 270 beetle prepupae). Data shown are means and standard errors of the difference variable used in the statistical test

prepupa (mean=32.9±1.0 mg) than in a pupa (mean=26 ±1.4 mg, $F_{1,55}$=15.6, P=0.0002).

Discussion

These experiments reveal that the phorid parasitoid *M. opacicornis* is attracted to the defensive larval secretion of its host and that the secretion elicits fly oviposition. The fly appears to be attracted to a source of beetle secretion at short (shown in the laboratory) and longer distances (shown in the field), and removing secretion reduces the likelihood of oviposition. The reduced amount of secretion produced by beetle pupae and by beetles that had already been attacked by another parasitoid (*Cl. nitidiuscula*) may be responsible for subsequent reductions in oviposition by *M. opacicornis*. Thus, secretions that protect beetle larvae against generalist insect predators, spiders and birds (Pasteels et al. 1986; Palokangas and Neuvonen 1992; Topp and Bell 1992) appear to attract rather than repel this parasitoid. Our results are consistent with those of an earlier study that showed that *M. opacicornis* parasitism was more intense on SG-rich host plants (Zvereva and Rank 2003), and they suggest that parasitoids are quite sensitive to the amount of secretion emitted by the host.

Our field experiment on attraction of *M. opacicornis* to beetle defensive secretion was initiated when beetles were still in the larval stage, before they are attacked by this pupal parasitoid in nature. However, we still found that many *M. opacicornis* individuals were attracted to the source of secretion that we placed on willows before naturally occurring pupae were present. In addition, we found that the number of parasitoids attracted to the source of secretion was positively related to the population density of *Ch. lapponica* on a given willow (E. Zvereva, personal observation). This suggests that *M. opacicornis* parasitoids concentrate in patches of high host density well before the hosts reach the stage suitable for parasitoid attack. The spatial density dependence of parasitism by *M. opacicornis*, which was previously reported by Zvereva and Kozlov (2000) may be explained by the higher cumulative release of beetle secretion around willows where beetles are especially abundant. Patches densely populated by the leaf beetle seem to attract parasitoids from further away.

Field experiments show a stronger attraction of parasitoid flies to secretions of the host in the field than in laboratory trials. The number of eggs laid on hosts whose secretion had been removed was lower than the number of eggs on control hosts, but the difference was greater in the field than in the laboratory. In addition, avoidance of hosts parasitized by *Cl. nitidiuscula* was much more pronounced in the field than in the laboratory. One possible explanation for this difference between laboratory and field results is that beetle defensive secretions as olfactory search cues are more important for a long-distance search than for short-distance prey choice.

The amount of secretion also affects *M. opacicornis* oviposition. In laboratory trials, phorid females laid twice the number of eggs on prepupae than on pupae, possibly because prepupae still have larval defensive glands that contain relatively high amounts of secretion, while pupae possess very little secretion. This oviposition preference had important consequences for parasitoid performance: *M. opacicornis* offspring grew larger when their eggs were placed on prepupae than on pupae. Thus, parasitoids oviposit on the host where their offspring's performance is highest, and attraction to defensive secretion may function to increase the likelihood of attack at the stage that is most beneficial for parasitoid development. By preferring to parasitize beetle prepupae over pupae, *M. opacicornis* avoids another potential cost. If parasitoid attack occurs very late in the pupal stage, the host may hatch before the parasitoid completes its development (Godfray 1994). Perhaps for this reason, pupal parasitoids usually prefer to attack at early pupal stages and to feed on young pupae that are not fully differentiated (Chabora and Pimentel 1977).

The amount of secretion is important not only for locating hosts, but may also serve as an index of host quality. For *M. opacicornis*, avoiding beetle larvae that have already been parasitized by the tachinid *Cl. nitidiuscula* is critical, because tachinid parasitoids have nearly completed their development and consumed host resources at the time of *M. opacicornis* oviposition. Our results showed that no *M. opacicornis* larvae survived on hosts parasitized by *Cl. nitidiuscula*. Avoiding beetle prepupae parasitized by *Cl. nitidiuscula*, which produce little or no secretion, allows *M. opacicornis* to escape from competition with the other parasitoid. Thus, by distinguishing between hosts rich and poor in defensive secretion, *M. opacicornis* parasitoids can avoid ovipositing on less suitable hosts.

Previous studies have revealed that secretions of *Chrysomela* species and related beetles are attractive to larvae of specialist fly predators (*Parasyrphus* sp., family Syrphidae). Köpf et al. (1997) found that fly larvae vigorously attacked pieces of filter paper that had been soaked in beetle secretion or its components. In addition, *Parasyrphus* larvae used the odor of the secretion to locate potential hosts. Other studies have also shown *Parasyrphus* egg abundance to be greatest on the beetles' preferred host plants, where beetle larvae produce high amounts of defensive secretion (Rank and Smiley 1994; Rank et al. 1996). Pasteels and Rowell-Rahier (1992) and Blum (1994) pointed out that defensive secretions of chrysomelid larvae might backfire if predators use the secretion to locate their prey. The results of the present study indicate that in addition to specialist predators, parasitoids also use beetle secretions to find their host. Increased attacks by parasitoids must now be considered an additional predation cost of the larval secretions to leaf beetles.

Because *Chrysomela* species derive their defensive secretion from their host plants, the effect of the secretion on natural enemies may influence relationships between the herbivores and their host plants. Some authors have suggested that pressure from natural enemies may have

contributed to specialization of these herbivores on toxic host plants (Pasteels et al. 1982; Smiley et al. 1985; Denno et al. 1990). However, very few experimental studies have supported the existence of enemy-free space for herbivores on SG-rich willows in nature (Smiley et al. 1985). Other studies have found little evidence that selection pressure from natural enemies favors a narrow herbivore diet breadth (Rank 1994; Rank et al. 1998). In an earlier study of *Ch. lapponica*, we showed that parasitism rates on beetle larvae were lower on SG-poor willows than on SG-rich ones (Zvereva and Rank 2003). The present study suggests that parasitism on SG-poor willows may be reduced because larvae feeding on these willows produce less defensive secretion, and might thus be less attractive to specialist parasitoids. Adaptations of parasitoids and specialist predators (Rank 1994; Köpf et al. 1997) to use the host plant-derived defensive secretion of prey as a kairomone may impose a selection pressure to increase the diet breadth of specialist herbivores to escape natural enemies (Rank et al. 1996). In this case, a specialist herbivore may obtain enemy-free space by increasing the breadth of its diet to include SG-poor willows (Lawton 1986; Rank et al. 1996; Gratton and Welter 1999).

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