

# The Impact of Herbivore-Induced Plant Volatiles on Parasitoid Foraging Success: A General Deterministic Model

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**Abstract** Parasitoids respond to volatiles that plants produce when injured by herbivores. A considerable body of literature addresses the chemical pathways of herbivore-induced volatile production. However, there is almost no theory or data on how timing of volatile release in relationship to host availability for parasitization impacts the utility of these cues to parasitoids and on the extent that this volatile release timing might increase or decrease the percent of herbivores that become parasitized. This kind of information is critical in judging the benefits that might accrue from a breeding program aimed at enhancing herbivore-responsive volatile production. We developed a general model to begin examining this issue by using available parameters from two tritrophic systems. The model uses herbivore oviposition, development, and mortality rates, linked to a range of plant volatile induction and cessation periods for calculating the proportion of plants in a field that are (1) not producing volatiles but occupied by suitable herbivore hosts, (2) producing volatiles and occupied by suitable herbivore hosts, (3) producing volatiles but not occupied by suitable herbivore hosts, and (4) not producing volatiles and not occupied by suitable herbivore hosts. The impact of the plant volatiles on parasitoid foraging success is then determined by comparing the expected number of hosts parasitized when the parasitoid focuses solely on the volatile-producing plants to when it forages randomly among all plants. Under some conditions, parasitoids can attack three times more herbivores if they focus on volatile-producing plants.

However, when we simulate plants that take several days to cease volatile production after pupation or death of the herbivore, parasitization rate does not increase when parasitoids use volatiles as cues. The utility of the volatile cues is consistently greater when a smaller proportion of plants is occupied by herbivores, indicating that their usefulness may be reduced to zero in fields saturated with volatiles.

**Keywords** Herbivore-induced plant volatiles · Tritrophic interactions · Parasitoid behavior · Deterministic model · Signal utility · *Heliothis virescens* · *Pieris rapae*

## Introduction

Plant volatiles induced by herbivory have been documented in numerous systems (Karban and Baldwin 1997). There are many examples of parasitoids orienting to herbivore-induced plant volatiles as a means of finding hosts, both in the field (e.g., DeMoraes et al. 1998; Oppenheim and Gould 2002) and in wind tunnels (e.g., Kaiser and Carde 1991; DeMoraes and Lewis 1999). One hypothesis about the evolution of this plant/parasitoid interaction suggests that plants evolve volatile production because those genotypes that produce herbivore-induced volatiles are more successful in attracting predators/parasitoids and therefore have higher fitness (Janssen et al. 2002). In contrast, a simpler hypothesis holds that plants produce herbivore-induced volatiles as a by-product of plant biochemistry and that parasitoids happen to have receptors that enable detection of these volatiles (Agrawal and Karban 1999). The value of attraction is hypothesized to be determined by the relative reliability and detectability of the plant signal (Vet et al. 1991). While host cues are under

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selection to be as undetectable as possible, plant cues are not under such selection. Parasitoids that are attracted to these cues are rewarded when these cues are a reliable indicator of presence of a suitable host.

However, even though plant cues are not directly selected against, they may not always provide a reliable signal to parasitoids. One potential source of misleading signals occurs when plants produce similar volatiles in response to a number of herbivore species, only some of which are hosts of a specific parasitoid (Rose et al. 1998; van Poecke et al. 2003). Another occurs when parasitoids respond to plants when the inducing herbivore is either too old to be attacked (Mattiacci and Dicke 1995; Brodeur and Vet 1995) or has left the plant (Mattiacci et al. 2001). The aim of this paper is to examine the extent to which variation in timing of volatile emission impacts utility of these cues for parasitoids.

In addition to natural sources of temporally misleading signals, crop breeding for over-expression of volatiles may produce situations where parasitoids gain less from response to the volatile. There has been considerable interest in breeding plants to produce increased quantity and quality of volatiles (Bottrell et al. 1998; Degenhardt et al. 2003; Lou et al. 2006). It is also possible that properly timed, increased volatile quantity could improve the efficiency of biological control agents by allowing parasitoids to target their foraging only to damaged plants with little cost to the plants. Initial investigations show the metabolic costs to the plant may not be significant enough to rule out breeding for constitutive volatile production. Several papers that propose this strategy mention that plant signals should be synchronized with herbivore presence to avoid a “calling wolf” scenario (Bottrell et al. 1998; Degenhardt et al. 2003); however, none specifies precisely how plant signals need to be synchronized. While a number of studies examine the chemical pathways plants use to produce signals (e.g., Kessler and Baldwin 2002), there are no published reports that we could find elucidating the regulation of specific genes that turn off volatile production when herbivory ceases.

As demonstrated by Holling (1959), predator and parasitoid foraging success is limited by three parameters: handling time, total available foraging time, and host encounter rate. Predators and parasitoids can take advantage of many visual, olfactory, and auditory cues in their environment to optimize host encounter rate. If herbivore-induced volatiles from plants can be used by the parasitoid to optimize these three parameters, then response to the volatiles can increase parasitoid foraging success. On the other hand, if parasitoid response to the volatiles increases handling time, decreases the available foraging time, or decreases the host encounter rate, response to induced volatiles could become less valuable.

The number of systems in which parasitoids are attracted to herbivore-induced plant volatile signals indicates that there must be some advantage to this attraction behavior; however, the few studies that quantify the fitness advantage parasitoids gain by following volatiles tend to focus on patch abandonment and modulating giving-up time (Vos and Hemerik 2003) rather than parasitoid attraction to individual plants in a larger environmental context. One purpose of this paper is to use modeling to examine the extent to which both the herbivore’s life history and the temporal pattern of the plant’s response to herbivory determine the benefit to the parasitoid of responding to herbivore-induced plant volatiles. Modeling has been instrumental in identifying other key aspects of parasitoid–host interactions, such as the value of refuges and asynchrony in parasitoid–host population dynamics (Takagi 1999).

The structure of the model is based on an extension of the Holling predation equation (Holling 1959). Life history and behavioral traits of two specific tritrophic systems that are potential candidates for genetic modification of volatile signal production were used in setting default parameters in our model. The first consists of tobacco, *Heliothis virescens*, and *Cardiochiles nigriceps*. De Moraes et al. (2001) found that female moths avoided ovipositing on plants emitting herbivore-induced volatiles, so for this system, we examined the consequences for parasitoid wasps if moths limit their oviposition to uninfested plants. The second system consists of *Brassica oleracea*, *Pieris* spp., and *Cotesia glomerata*. Females of the parasitoid *C. glomerata* are attracted to plant volatiles induced by all instars of *P. brassicae* (Mattiacci and Dicke 1995); however, parasitoid larvae suffer greater mortality due to increased encapsulation if laid in third or later host instar caterpillars. Geographically isolated populations of *C. glomerata* vary in their foraging behavior and host range (Vos and Vet 2004). Given the general nature of the model developed here, we did not address intraspecific variation, and we used data from congeneric species when needed. We used our model to examine the consequences of narrowing the window of available host instars that a parasitoid could attack. While parameter values from these two tritrophic systems were used as starting points, we also explored a wider set of parameter values to gain a broader understanding of the impacts of signal–host synchronization.

Overall, we expected that signals more closely synchronized with host presence would be more relevant to foraging parasitoids, so that plants in a field that could respond to herbivory in 1 day would produce more relevant signals than plants that took 5 days. However, before analysis with this model, we did not know whether the cost of delaying a signal from 1 to 5 days would be substantial or hardly noticeable. Similarly, while we expected herbivore density to impact the relevance of the volatiles to

parasitoids, we did not know whether this would be a major or a minor effect. Our use of general characteristics of two systems, with varying herbivore life histories, allowed us to identify what variables were more sensitive to initial conditions when predicting the relevance of volatiles to parasitoids. A companion paper describes a more detailed stochastic and spatial model of the interactions between *Cotesia rubecula* and *P. rapae* (Puente et al. 2008, following paper).

### Methods and Materials

*Incorporating Plant Volatiles into Holling's Equation* The fitness of a solitary parasitoid can be correlated directly with the number of hosts successfully attacked, as each host can lead to one offspring. Therefore, the relevance of herbivore-induced plant signals can be defined as a ratio of the number of hosts attacked if a parasitoid follows signals, compared to if it randomly forages with respect to plant signals.

$$Rel = \frac{N_{ASig}}{N_{ARan}} \quad (1)$$

where *Rel* is the signal relevance to the parasitoid,  $N_{ASig}$  is the number of hosts attacked by parasitoids that focus only on plants that are producing herbivore-induced volatile signals, and  $N_{ARan}$  is the number of hosts attacked by randomly searching parasitoids. If *Rel* is equal to 1, either foraging method yields the same fitness; if  $Rel > 1$ , then a parasitoid is more efficient by responding to plant signals, and if  $Rel < 1$ , then the parasitoid is more efficient when it ignores plant signals.

The predation equation developed by Holling (1959) provides a way of predicting the number of prey (or hosts in this case) attacked, given the predator's (or parasitoid's) behavior and the host density.

$$N_A = \frac{T_t \times a \times x}{1 + a \times b \times x} \quad (2)$$

where  $T_t$  is the total time available for foraging, *a* is the "instantaneous rate of discovery," *b* is the handling time for a single oviposition, and *x* is the density of hosts. If we substitute this into the previous equation, we get

$$Rel = \left( \frac{T_t \times a_{Sig} \times x_{Sig}}{1 + a_{Sig} \times b_{Sig} \times x_{Sig}} \right) / \left( \frac{T_t \times a_{Ran} \times x_{Ran}}{1 + a_{Ran} \times b_{Ran} \times x_{Ran}} \right) \quad (3)$$

The definitions of the variables in the Holling equation and the units of measure are system-specific. In our model, we can assume that the induction phenomenon occurs systemically throughout a plant (e.g., Mattiacci et al. 2001) and that it is constrained to a single plant. The density of

hosts, *x*, in the Holling model is traditionally provided in hosts per square meter, but because induction is occurring at the level of plants, not meters, we assume one plant per square meter and thus give our density measurements in "hosts/plant."

The total time available  $T_t$  is the amount of time the parasitoid remains foraging in the relevant environment. We assume that  $T_t$  is for a single day and that the parasitoid forages only in the field of interest for that day, thus giving us a daily attack rate. To keep all time units equal,  $T_t$  is measured in seconds.

The instantaneous rate of discovery *a*, also known as the area of discovery, is traditionally given in the units of area per unit of time (the lower case "a" should not be confused with upper case "A" in  $N_A$ , which is the total attack rate). We are interested in how many plants the parasitoid can visit rather than the area that can be covered; therefore, we make a few assumptions about the area of discovery. We assume that the parasitoid forages by visiting the nearest neighboring plant or, in the case of following volatile signals, the nearest neighboring signaling plant. To calculate the area of discovery, *a*, for randomly foraging parasitoids, we take the parasitoid flight speed (in meters per second) and multiply by the density of plants (plants per meter). Multiplying  $T_t$  by *a* gives the maximum number of plants a parasitoid can visit during the total foraging time. Multiplying that result by *x* gives the maximum number of hosts the parasitoid could possibly encounter if no time were required to find and handle the host once the parasitoid arrived at a plant.

Because a fraction of that total time is spent in handling hosts, the actual number of the hosts attacked is less than the maximal number of plants that the parasitoid could encounter. The more plants encountered, the more time that must be invested in both searching for and handling hosts. The handling time, *b*, is the amount of time the parasitoid spends from the time it encounters a host to the time it stops handling the host. Because this model follows just a single host per plant, the parasitoid is assumed to leave the plant immediately after handling the host. However, in cases where multiple larvae could be encountered on a single plant, *b*, the term we add to describe on-plant searching, could be modified with functions to describe continued on-plant searching behavior. The total time spent in handling hosts is  $a \times b \times x$ . The actual number of plants a parasitoid can visit is then  $a \times x \times$  the time available for searching, which is only a fraction of the total time available for foraging. This fraction can be calculated as  $T_t / (1 + a \times b \times x)$ .

However, this assumes that handling time is fixed for each encounter. While the time it takes for a parasitoid to sting a found host may be equal regardless of the plant's state, the amount of handling time a parasitoid searches a plant before finding (or giving up on) a host may depend on

how the parasitoid perceives the plant state. For example, when encountering herbivore-induced plant volatile cues, some parasitoids search plants longer before leaving (Nealis 1990; Horikoshi et al. 1997; Sato and Ohsaki 2004). By prolonging a parasitoid’s giving-up time, herbivore-induced plant volatiles can impact the time budget for foraging parasitoids. To account for a difference in giving-up time, as part of the overall handling time, we modified the Holling equation as follows:

$$N_A = (T_i \times a \times x) / (1 + a \times b \times x + a \times c \times E + a \times c / 2 \times O) \tag{4}$$

Where  $c$  is the giving-up time per plant,  $E$  is the proportion of plants that are empty of hosts, and  $O$  is the proportion of plants in the field that are occupied by a host. The total time a parasitoid must devote to searching if no herbivore is present is  $a \times c \times E$ , which is the probability of a parasitoid landing on an empty plant ( $a \times E$ ) multiplied by the rate of giving-up time per arresting plant. If an herbivore is present ( $O$ ), we assume that the searching time ceases as soon as the host is found. If we assume that the probability that the host is found per unit time is the same from the instant that a parasitoid lands up to the moment the search time expires, then the average time spent will be half the giving-up time. Therefore, the time spent searching occupied plants is  $a \times c / 2 \times O$ .

Given these definitions of the variables, we can ask how a parasitoid’s decision to follow or ignore induced plant volatiles can change the values of these variables. There have been many hypothesized mechanisms through which herbivore-induced plant volatiles can influence parasitoid foraging. For example, parasitoids may change their turning radius (Kareiva and Odell 1987), alter their flight speed (Norlund 1981), or change their total time budget to spend more time feeding per day (Siekmann et al. 2004). While our model is flexible enough to examine these hypotheses, in this paper, we will explore only the impact of parasitoids bypassing non-signaling plants on signal relevance; for further exploration of the model, see Puente (2007).

By identifying the preferred host–plant complex out of a mixed background, parasitoids can bypass uninformative plants. When the parasitoid bypasses non-signaling plants, we assume it maintains the same flight speed and handling time but restricts its environment to signaling plants only. In natural settings, a parasitoid may also pick up on other cues (such as herbivore frass) that may induce it to

investigate non-signaling plants but that is beyond the scope of this model. The parasitoid may, therefore, encounter a different density of hosts if it preferentially forages on signaling plants rather than foraging randomly. The impact this has on the signal relevance depends on the underlying host density and the plant signal reliability.

At any point in time, a plant could be in one of four possible qualitative states. Individual plants are either emitting volatiles that could act as signals (S) or not emitting (N) and are either occupied (O) by a suitable herbivore host or empty (E) of a suitable host; thus, a plant’s state can be NO, NE, SO, or SE. While a single plant does not retain its state for an entire season, a field may reach an equilibrium distribution of plants in those four categories.

A parasitoid responding to plant signals perceives the host density as the number of SO plants ( $n_{SO}$ ) divided by the sum of all signaling plants ( $n_{SO} + n_{SE}$ ), while a parasitoid randomly foraging perceives the host density as the sum of all occupied plants ( $n_{SO} + n_{NO}$ ) divided by the total number of plants in the field. Mathematically,

$$x_{Sig} = n_{SO} / (n_{SO} + n_{SE}) \tag{5a}$$

$$x_{Ran} = (n_{SO} + n_{NO}) / (n_{SO} + n_{NO} + n_{SE} + n_{NE}) \tag{5b}$$

All other variables being held constant, if ( $x_{Sig} > x_{Ran}$ ), signal relevance will be greater than one, and if ( $x_{Sig} < x_{Ran}$ ), signal relevance will be less than one. However, because density is not linearly correlated with signal relevance ( $x$  appears in both the numerator and the denominator), the magnitude of this advantage in terms of number of hosts attacked depends on the actual values of  $n_{SO}$ ,  $n_{NO}$ ,  $n_{SE}$ , and  $n_{NE}$ .

Additionally, these four states impact the values of  $E$  and  $O$  in Eq. 4, so if we include arrestment in our equations, we can make the following substitutions:

$$E_{Sig} = n_{SE} / (n_{SO} + n_{SE}) \tag{6a}$$

$$E_{Ran} = (n_{SE} + n_{NE}) / (n_{SO} + n_{NO} + n_{SE} + n_{NE}) \tag{6b}$$

Additionally, we can substitute Eq. 5a and 5b for  $O$  in both the signaling and randomly foraging equations.

When we have finished making these substitutions, we have the following equations:

$$N_{ASig} = \frac{T_i \times a_{Sig} \times \left( \frac{n_{SO}}{n_{SO} + n_{SE}} \right)}{1 + a_{Sig} \times b_{Sig} \times \left( \frac{n_{SO}}{n_{SO} + n_{SE}} \right) + a_{Sig} \times c_{Sig} \times \left( \frac{n_{SE}}{n_{SO} + n_{SE}} \right) + a_{Sig} \times \frac{c_{Sig}}{2} \times \left( \frac{n_{SO}}{n_{SO} + n_{SE}} \right)} \tag{7}$$

$$N_{ARan} = \frac{T_1 \times a_{Ran} \times \left( \frac{n_{SO} + n_{NO}}{n_{SO} + n_{SE} + n_{NO} + n_{NE}} \right)}{1 + a_{Ran} * b_{Ran} * \left( \frac{n_{SO} + n_{NO}}{n_{SO} + n_{SE} + n_{NO} + n_{NE}} \right) + a_{Ran} \times c_{Ran} \times \left( \frac{n_{SE} + n_{NE}}{n_{SO} + n_{SE} + n_{NO} + n_{NE}} \right) + a_{Ran} \times \frac{c_{Ran}}{2} \times \left( \frac{n_{SO} + n_{NO}}{n_{SO} + n_{SE} + n_{NO} + n_{NE}} \right)} \quad (8)$$

Finally, when parasitoids bypass non-signaling plants, we assume that the parasitoid’s flight speed does not change, but the distance between perceived nearest neighbors increases. The area of discovery for parasitoids following signals must be adjusted to account for the increase in distance:

$$a_{Sig} = a_{Ran} \times \sqrt{\frac{n_{SO} + n_{SE}}{n_{SO} + n_{SE} + n_{NO} + n_{NE}}} \quad (9)$$

If we assume that our field is square, then the number of plants in each row is the square root of the total number of plants in the field (the sum of the number of plants in the four states). Likewise, if we assume the signaling plants are distributed equally between the rows, then the number of signaling plants per row is the square root of the total number of signaling plants (the sum of the number of plants in SO and SE states). If we assume that the parasitoid forages along a straight path, then the density of signaling plants encountered is the square root of the density of signaling plants in the field.

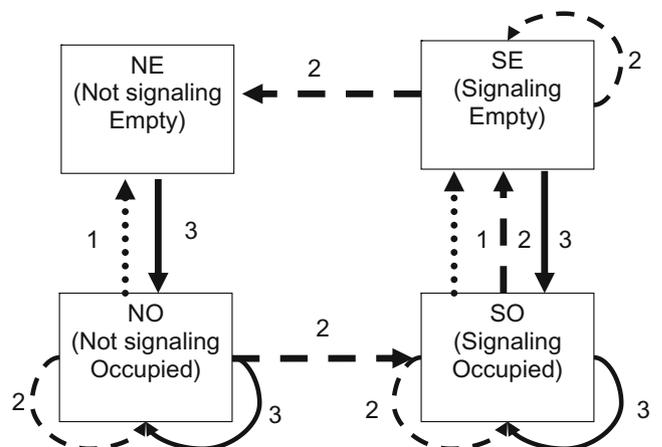
To understand what distribution of plant states may occur in natural populations, we use an age–class transition model for two herbivore examples. Figure 1 demonstrates transition of plants between the different states.

The model begins with all of the plants neither occupied nor induced (NE) and runs for 100 time steps. Each time step represents a single day. A set fraction of plants ranging from 0.1 to 0.9 are newly “occupied” by herbivores at each time step. For a lepidopteran herbivore, the occupation rate is equivalent to the rate of eggs hatching in a single day, which is equivalent to a daily oviposition rate, assuming there is no significant egg mortality. Occupation rate is expected to correlate with the proportion of plants infested. As plants become occupied, they move either from NE to NO or from SE to SO.

A plant remains occupied as long as a suitable larval host is feeding. Pupation, mortality, and dispersal are all potential ways for plants to be abandoned by larvae, and the probability of these events depends on the age of the larva. The maximum number of days a plant can remain infested by a single larva and thus the maximum number of infestation age classes is the development time for the herbivore larva. When larvae pupate, the plants on which they resided are moved into the SE class unless a plant is simultaneously occupied by a younger larva. When a parasitoid cannot attack an herbivore because it has matured beyond its vulnerable instars, the plant is consid-

ered “empty,” similar to what happens when the herbivore pupates; however, because the herbivore continues to feed, the plant continues to produce volatile signals. Because these unsuitable hosts are classified as empty, a parasitoid encountering these hosts spends no handling time (*b*) in the current model, but it would be appropriate to add handling time of unsuitable hosts in specific systems.

Because herbivore mortality rate depends on larval age, the model includes different infestation age classes for each day of larval occupancy. At each time step, each age class is multiplied by the appropriate mortality rate, which accounts for density-independent mortality sources for that larval age class such as weather and diffuse predation. The fraction of plants with dying larvae are moved into the SE state if they were on a signaling plant and moved into the NE plant state for non-signaling plants, while the remaining plants are advanced to the next infestation age class. For the systems



**Fig. 1** Flow diagram describing transitions between the four plant states, with each plant state represented by a box. Age classes of herbivores are modeled within each of the occupied (O) states, and relaxation rate-time classes are modeled within the signaling empty (SE) state (not shown). Each time step consists of the following three sequential operations: (1) Occupied plants are multiplied by the mortality rate, and the fraction of plants with dying larvae move to one of the two empty states (dotted line). (2) Larvae on occupied plants are matured by one time step (dashed line). Plants with larvae that become older than the induction time move from the not signaling occupied (NO) state to signaling occupied (SO) state, and plants with larvae that become pupae move from SO to the signaling empty (SE) state. Plants in SE long enough to turn off the signal moved from SE to the not signaling empty (NE) state. (3) All age classes and states are multiplied by the occupation rate (solid line) and the fraction of plants receiving new larvae have the larval age class set to 1

explored here, dispersal of larvae to other plants was not a major factor, so dispersal was left out, but when expanded to other systems, herbivore migration would both cause occupied plants to become empty and empty plants to become occupied.

When a plant is reinfested, it is classified by its youngest larva, i.e., placed in the first infestation age class, but remains in the “signaling” state if it was previously signaling. This allows for plants to remain signaling for longer than the time of a single larva’s development when multiple larvae reside on a plant. However, this introduces a potential bias to the model. In the situation in which the youngest larva dies before the others, the plant would be moved into the “empty” category before the plant was in fact abandoned. This bias is unavoidable because the model cannot follow the fate of individual larvae on each plant.

Although volatile production is probably a continuous function in real plants, we modeled it as a discrete binary function. This means that we assumed that the parasitoids have a perception threshold for volatile concentrations; a plant was “signaling” if it was producing enough volatiles to be perceived by the parasitoid and “not signaling” if the concentration was below the parasitoid’s perception threshold. In addition to describing induction as an “on–off” function, we assumed that the concentration of volatiles only changed at the beginning of a daily time step. The induction delay at which plants move from N to S after the onset of herbivory is set at values ranging from 1–5 d for this model. The relaxation delay at which plants move from S to N after the cessation of herbivory is also fixed at values ranging from 1–5 d.

This model can allow us to generate the proportion of plants in each state over time, and we can take these distributions and substitute them into Eqs. 7 and 8. Because we are primarily concerned with the impact of herbivore population density on signal relevance, we hold  $a$ ,  $b$ , and  $T_t$  constant, using parameters from the literature for the two-system examples we provide. For more information on the assumptions made in this model, see Puente (2007).

**Model Parameters** We used life history data on *H. virescens* and *P. rapae* for setting parameter values in the model. *H. virescens* is a generalist in the taxon Noctuidae and attacks many important crop plants including cotton and tobacco (Neunzig 1969). It has many well-known parasitoids and predators, both specialists and generalists. *C. nigriceps*, a parasitoid that attacks all stages of *H. virescens* larvae (Lewis and Vinson 1971), is preferentially attracted to *H. virescens* on certain host plants and can distinguish *H. virescens* infestations from infestations by closely related *Helicoverpa zea* (DeMoraes et al. 1998). In field studies, *C. nigriceps* preferred hosts on tobacco rather than on cotton, regardless of the dominant host plant

available (DeMoraes and Lewis 1999; Tillman and Mullinix 2003). While difference in volatile production may explain how parasitoids can distinguish between cotton and tobacco, it does not explain why *C. nigriceps* prefers tobacco. Understanding the temporal dynamics of induction may help us understand host preferences.

Daily mortality rates for *H. virescens* were calculated for each larval stage by using data from Johnson and Gould (1992). Because *H. virescens* varies widely in its survival rates, a low and a high mortality scenario are examined (see Table 2). *H. virescens* adults avoid ovipositing on plants that are already occupied by larvae or eggs (DeMoraes et al. 2001). Under the special case that adult herbivores avoid ovipositing on already-infested plants (“limited oviposition” condition), only plants in the NE state are multiplied by the occupation rate. When this assumption is lifted to allow the default multiple ovipositions on a plant (“multiple oviposition” condition), all plant age classes are multiplied by the occupation rate. Both oviposition scenarios are considered for this herbivore.

Parameter values for *C. nigriceps* were obtained from Tillman and Mullinix (2003) and are summarized on Table 1. The parasitoids are typically active between 0900 and 1500 hours, and spend about half of that time engaged in host foraging behaviors, which translates to a  $T_t$  of 3 hr or 10,800 sec. On the host plant tobacco, parasitoids spend 11.6 sec hovering and 11.7 sec searching around a plant for a total of 23.3 sec searching per plant, giving an estimate of

**Table 1** Variables in the model

Parameter	<i>Heliothis virescens</i>	<i>Pieris rapae</i>
	<i>Cardiochiles nigriceps</i>	<i>Cotesia glomerata</i>
$T_t$ (sec)	10,800 <sup>a</sup>	14,400 <sup>b</sup>
$a$ (plant/sec)	0.043 <sup>a</sup>	0.33 <sup>c</sup>
$b$ (sec/hosts)	20.5 <sup>a</sup>	13.1 <sup>d</sup>
$c$ (sec/plant)	128.7 <sup>a</sup>	73.5 <sup>d</sup>
Occupation rate (new larvae/total plants/day)	0.1–0.9	0.1–0.9
Induction delay (days)	1–5	1–5
Relaxation delay (days)	1–5	1–5
Oviposition <sup>e</sup>	Limited and multiple	Multiple
Host attack stage (instar)	5	1–5

<sup>a</sup> Tillman and Mullinix 2003

<sup>b</sup> Kaiser and Cardé 1991

<sup>c</sup> Kaiser et al. 1994

<sup>d</sup> Sato and Ohsaki 2004

<sup>e</sup> ‘Oviposition’ refers to whether the host limits oviposition to plants that are neither occupied nor signaling (Limited) or will place multiple larvae on one plant (Multiple).

0.043 plants per second for *a*. The handling time for oviposition and preening (*b*) was 20.5 sec per host. Finally, the time spent in what Tillman and Mullinix (2003) refer to as “agony search,” a measure of the giving-up-time estimate for *c*, was estimated to be 128.7 sec for wasps on tobacco.

The *P. rapae* tritrophic system has been extensively studied both because it is tractable and because it has economic relevance for many crops. *P. rapae* is a butterfly in the taxon Pieridae that specializes on brassicacean plants, including crops such as cabbage, broccoli, and Brussels sprouts, and the experimental model system, *Arabidopsis thaliana* (Courtney 1986). A major larval parasitoid for *P. rapae* in some geographic areas (Vos and Vet 2004), *Cotesia glomerata*, is restricted to surviving in only the early instars of *P. rapae* but cannot distinguish the age of the larvae based on plant volatiles alone (Mattiacci and Dicke 1995). The temporal pattern of herbivore-induced plant volatile production has been documented only for a few systems, including *P. rapae*. Geervliet et al. (1998) found that Brussels sprouts were most attractive to braconid parasitoids after 3 d of feeding by *P. rapae*. Additionally, a wind tunnel study found that Brussels sprouts fed on by *P. brassicae*, a close relative to *P. rapae*, were most attractive to *C. glomerata* 3 d after feeding and ceased being attractive to the parasitoids 1 d after the herbivores were removed (Mattiacci et al. 2001).

*P. rapae* larvae go through five instars of approximately 3 d each. Daily mortality rates were taken from Dempster (1967; see Table 2). Because *C. glomerata* survives only on the first two instars, in this model, encountering a plant

with a fifth instar larva would have the same effect as encountering an empty plant because no host could be attacked. To simulate this system, the mechanisms for classifying signaling from non-signaling states as described previously were maintained, but the definitions of empty and occupied were reassessed to include the parasitoid’s age preference. The term “attack preference” refers to the maximum age of larva a parasitoid is able to attack successfully. We examined the impact that attack preference has on signal relevance by setting the attack preference at 3 d (first instar), 6 d (second instar), 9 d (third instar), 12 d (fourth instar), and 15 d (fifth instar). It is possible that parasitoids encountering a host that is beyond the attack preference may spend more or less time investigating before leaving the plant (and thus “*c*” would not be the same as it would for a truly empty plant), but we chose not to consider those special conditions in this initial model.

To calculate signal relevance for this system, we can use parameter estimates derived from the literature (see Table 1). The parasitoids are most active in the late morning and early afternoon (Kaiser and Carde 1991), so we assumed a maximum of 4 hr of foraging per day; the total time (*T<sub>i</sub>*) is 14,400 sec. Sato and Ohsaki (2004) observed that, for *C. glomerata* searching for *Pieris* larvae, the time spent searching one leaf (*c*) was 73.5±11.9 sec, and the handling time (*b*) was 13.1±3.9 sec. We can use the mean of these observations as our parameter estimates. The recorded flight speed for *C. rubecula*, a closely related species that also parasitizes *P. rapae*, was 0.33 m/sec (Kaiser et al. 1994), so we can use this to estimate the parameter *a*; area of discovery as 0.33 plants per second.

**Table 2** Daily mortality of larvae as a proportion of the individuals at a specific age within a larval instar

<i>Heliothis virescens</i> <sup>a</sup>				<i>Pieris rapae</i> <sup>b</sup>	
Day	Instar	Low mortality	High mortality	Instar	Mortality
1	1	0.12	0.33	1	0.187
2	1	0.12	0.33	1	0.187
3	1	0.12	0.33	1	0.187
4	1	0.12	0.33	2	0.087
5	2	0.03	0.26	2	0.087
6	2	0.03	0.26	2	0.087
7	2	0.03	0.26	3	0.084
8	3	0.03	0.21	3	0.084
9	3	0.03	0.21	3	0.084
10	3	0.03	0.21	4	0.137
11	4	0	0.03	4	0.137
12	4	0	0.03	4	0.137
13	4	0	0.03	5	0.233
14	5	0	0	5	0.233
15	5	0	0	5	0.233
16	5	0	0	0	0
Cumulative		0.51	0.96		0.91

<sup>a</sup> Johnson and Gould 1992

<sup>b</sup> Dempster 1967

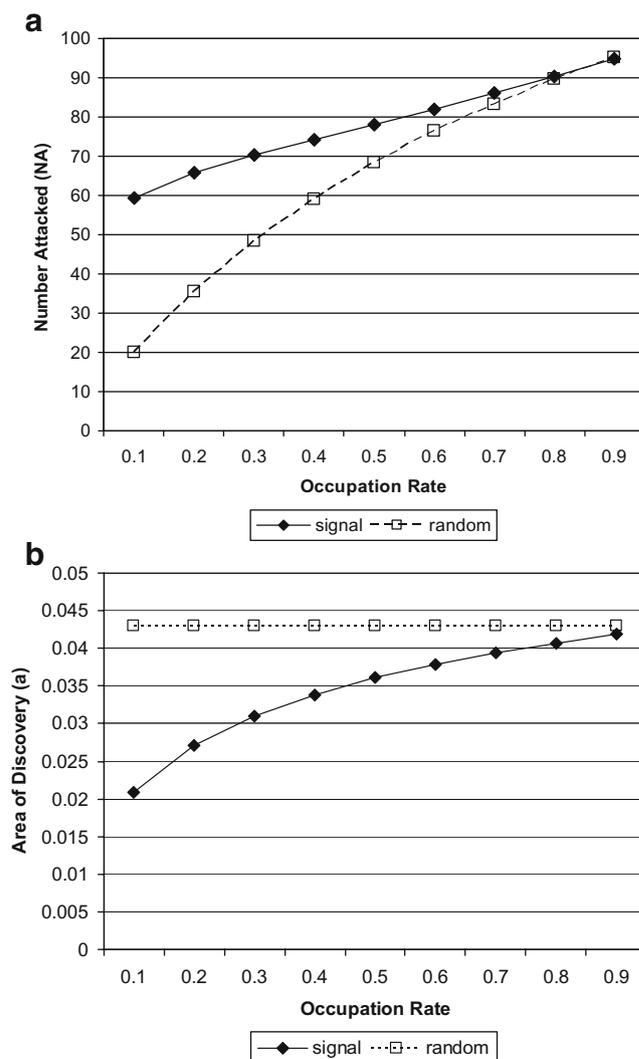
## Results

**Fixed Parameters** Total foraging time, handling time, area of discovery for random foraging, and giving-up time were held constant for all simulations investigated for a particular herbivore system. Handling time and giving up time were shorter for the *Pieris* system, while area of discovery and total foraging time were shorter for the *Heliothis* system. This leads us to predict that for one foraging day, *Cotesia glomerata* would be capable of attacking more *P. rapae* than *C. nigriceps* is capable of attacking *H. virescens*. In fact, if we set all other parameters (induction delay, relaxation delay, host attack preference, occupation rate, high mortality) equal, then the  $N_A$  for *Pieris* is between two and four times as large as  $N_A$  for *Heliothis*. However, when all other parameters are equal, there is not a considerable difference in signal relevance between the *Pieris* and *Heliothis* systems, except at the lowest occupation rates when, for example, if plant signal delays are both held at 1 day, a parasitoid of *H. virescens* could see a threefold improvement by following plant cues, compared to only a 2.5-fold improvement for parasitoids of *P. rapae*. This means that even though more *P. rapae* larvae can be attacked per day, parasitoids for both herbivores have the same threshold for when they should not follow cues.

**Occupation Rate** As occupation rate increases, the proportion of plants occupied increases but approaches an asymptote rather than being linearly correlated with occupation rate. The asymptote is a product of the model design. Plants are infested by multiplying each stage class by the occupation rate, ensuring that a fraction of plants will remain unoccupied for any occupation rates less than 1. At very high occupation rates, the proportion of plants unoccupied can be infinitesimally small so that, in a real field, all plants would in fact be occupied. As described in “Methods and Materials,” the fact that the multiple oviposition scenario reaches an asymptote below 1.0 is a result of the model following only the youngest larva on a plant. In the limited oviposition scenario, the asymptote is at an even lower proportion due to the ovipositing host’s avoidance of plants induced and empty (SE). Although this may make the model less realistic for natural outbreak conditions, in agricultural settings, growers would be advised to spray long before 90% of the field is occupied; therefore, our model is acceptable over the range to probable herbivore infestation rates.

One consistent trend for most parameter combinations is that, as occupation rate is increased from 0.1 to 0.9, the  $Rel$  value decreases. As occupation rate increases, the proportion of plants infested increases, so the number attacked ( $N_A$ ) increases for both wasps following signals and wasps

randomly foraging. However, the patterns of increase differ between the foraging strategies (Fig. 2a). The  $N_A$  for random foraging increases after a type II functional response, with a large initial increase in attacks slowing down as handling and giving up time become a greater limitation. We see this type II response because occupation rate regulates the transition from NE to NO, and thereby directly changes the density of occupied plants (Eq. 5b). The  $N_A$  for parasitoids that respond only to signaling plants, however, does not increase as drastically. The transition from SO to SE is primarily due to the mortality rate, so changing the occupation rate does not change the density of occupied signaling plants compared to all signaling plants



**Fig. 2** The impact of occupation rate. These sample data came from the parameters of high mortality and multiple oviposition for *H. virescens*, and plant induction and relaxation delays of one day each. **a** The relationship between occupation rate and number of hosts attacked ( $N_A$ ) for parasitoids following signals (signal) compared to parasitoids randomly foraging (random). **b** The relationship between occupation rate and area of discovery ( $a$ ) for parasitoids following signals (signal) compared to parasitoids randomly foraging (random)

(Eq. 5a). However, an increase in occupation rate does change the density of occupied signaling plants compared to all plants (Eq. 9), which results in an increasing area of discovery as occupation rate increases (Fig. 2b). Additionally, in the case of multiple oviposition by *H. virescens*, the chance of a signaling plant being reinfested before relaxing the signal increases with greater occupation rates, which also can lead to a modest increase in density of signaling plants with increasing occupation rates. At high occupation rates, virtually all plants that are occupied are also signaling, resulting in *Rel* approaching one. The only exception to these general patterns was in the case of setting host attack stage to first instars, which will be discussed in the section on host-stage attack.

For the remainder of this paper, we present results for occupation rates less than 0.5, as data for higher occupation rates both represent unrealistic field densities and are less reliable due to the inherent bias in the model toward younger larvae when plants are multiply occupied.

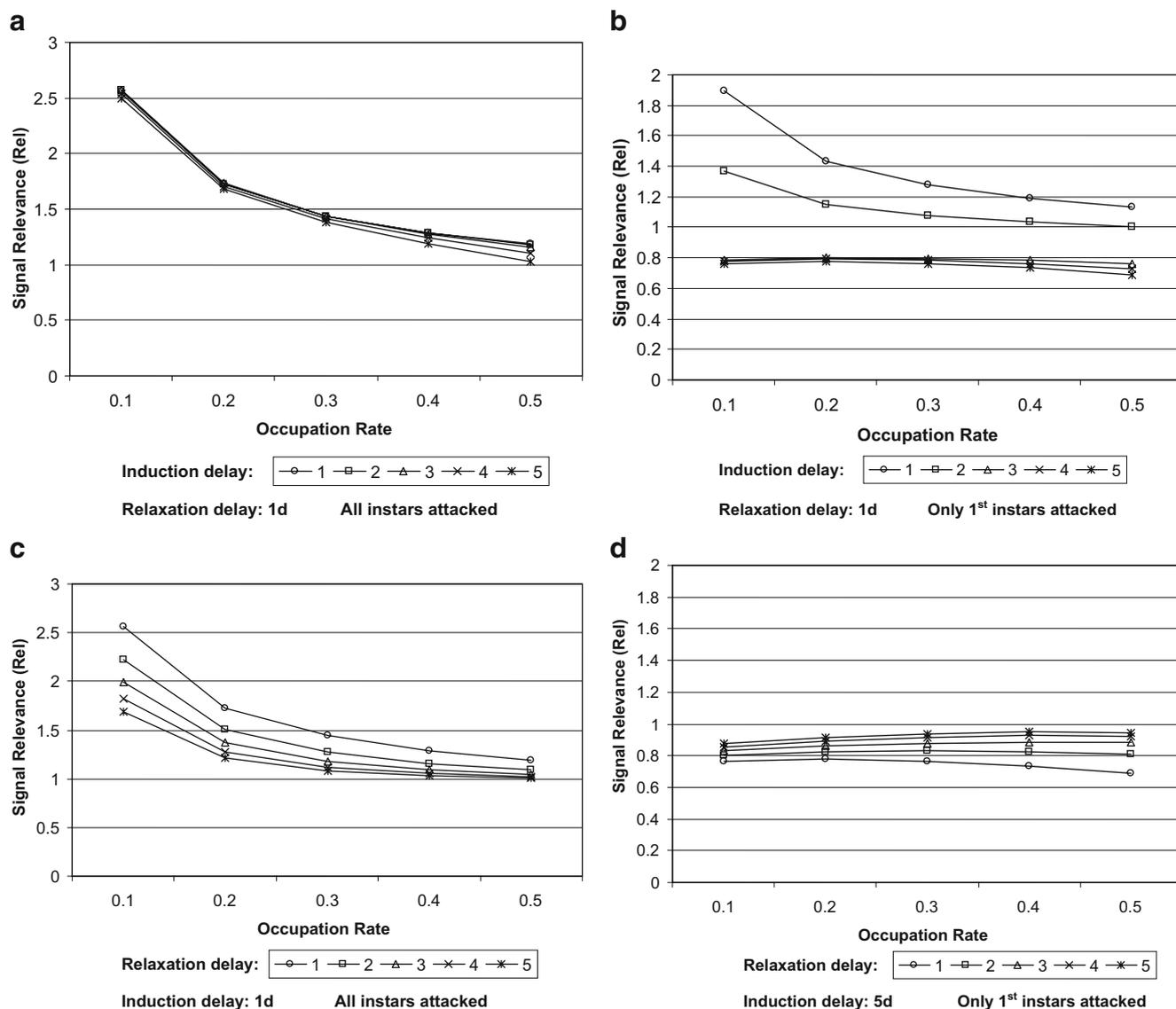
**Induction Delay** While we are presenting the data only for the *Pieris* system, the impact of induction delay was similar for both *Heliothis* and *Pieris* systems. In most cases, varying induction delay from 1 to 5 d resulted in less than a 0.1 difference in *Rel* values (Fig. 3a). Induction delay determines the transition from NO to SO plants; for randomly foraging parasitoids, this does not change the density of hosts because NO and SO appear in both the numerator and denominator of the density calculations (Eq. 5b). For signal-following parasitoids, once plants are in SO, the transition to SE is not dependent on the induction period, so this does not change the density of available hosts (Eq. 5a). A change in ratio of SO to NO plants can impact the area of discovery, and therefore, we see that a 5-d induction delay leads to a lower *Rel* than a 1-d induction delay, but the change is small, and the parasitoid would benefit from following signals regardless of the induction delay. It should be noted that this result rests on the assumption that the resources in the field are infinitely abundant, so that even though signaling plants are rare in the field, there is still a large enough number of plants in the field to exhaust the parasitoid's total foraging time. The only exception to this general pattern was in the case of setting host-attack stage to first or second instars, which will be discussed in the section on host-stage attack (Fig. 3c).

**Relaxation Delay** In most cases, as the delay for plant signal relaxation increased from 1 to 5 d, the relevance of the signal decreased (Fig. 3b); the only exception was the case when host-stage attack was limited to first instars (Fig. 3d). Relaxation delay determines the transition of plants from SE to NE. A long delay increases the number

of plants remaining in the SE state, which has the effect of lowering the relative density of occupied signaling plants without changing the overall density of occupied plants. In other words, a long relaxation delay means that parasitoids following signals will spend more time foraging on unoccupied plants, thus decreasing the number of hosts attacked.

For the *Heliothis* system, we compared signal relevance when oviposition was limited to empty plants and when there was no limitation. When multiple ovipositions per plant are allowed, the impact of relaxation delay decreases at higher occupation rates because signaling plants are likely to be reinfested. However, when oviposition is limited, the effect of relaxation delay continues even at higher occupation rates.

**Mortality Rate** Because reported mortality rates vary greatly for *H. virescens*, we looked at the impact of herbivore mortality for that system only. At low occupation rates, signal relevance was higher when the host mortality rate was higher (Fig. 4); however, at higher occupation rates, lower mortality led to higher signal relevance. Mortality can either cause plants to shift from NO to NE states or from SO to SE states, and the impact of mortality on signal relevance depends on the balance of these two transitions. A transition from NO to NE will decrease the density of occupied plants while having no effect on the density of signaling plants that are occupied; thus,  $x_{\text{Sig}}$  will not be affected by the transition but  $x_{\text{Ran}}$  will. However, the transition from NO to NE also limits the number of plants in the NO state that can then enter the SO state, thus reducing the  $n_{\text{SO}}$ , which has the effect of decreasing  $a_{\text{Sig}}$ . A transition from SO to SE will decrease both the overall density of occupied plants and the density of signaling occupied plants. Because mortality is concentrated at the earliest part of the *H. virescens* life table, the number of transitions from NO to NE is greater than from SO to SE, and therefore, initially increasing mortality causes an increase in signal relevance. In other words, at low occupation rates, the distance between signaling plants is so great that a parasitoid stopping at an empty signaling plant is at a great disadvantage; when mortality is high, herbivores die before plants begin signaling, thus reducing the number of false signals in the field. However, once the herbivore density becomes high enough so that the area of discovery is similar for both foraging strategies, the impact that mortality has on herbivore density becomes much more important. The number of signaling plants is less than the number of plants in the field, and, therefore, the transition of a single plant due to herbivore mortality will have a greater impact on the signaling density than on the overall density. Increasing the mortality decreases the signal relevance as occupation rate increases.

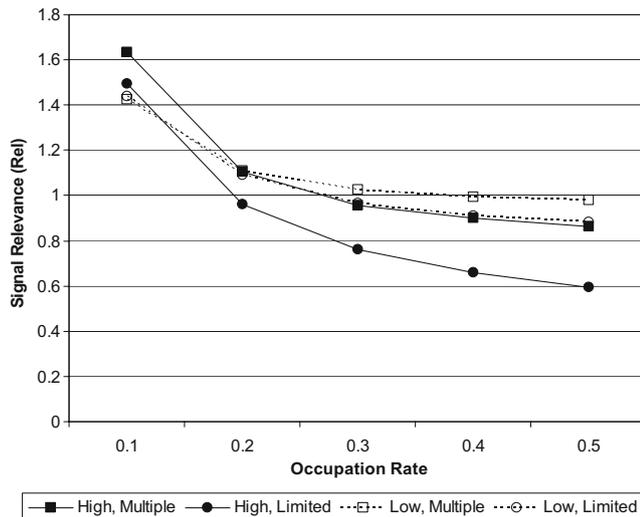


**Fig. 3** The relationship between induction delay, relaxation delay, host-stage, attack preference, and signal relevance. For all four cases shown, mortality rates and parasitoid foraging parameters were set to resemble those of *P. rapae* and *Cotesia glomerata*. **a** Numbers in the legend reflect days for induction delay. Relaxation delay was fixed at 1 d. Host-stage attack preference was fixed at fifth instar. **b** Numbers in the legend reflect days for relaxation delay. Induction delay was

fixed at 1 d, and host-stage attack preference was fixed at all instars attacked. **c** Numbers in the legend reflect days for induction delay. Relaxation delay was fixed at 1 d. Host-stage attack preference was fixed at first instar. **d** Numbers in the legend reflect days for relaxation delay. Induction delay was fixed at 5 d, and host-stage attack preference was fixed at first instar

**Oviposition Preference** We only tested oviposition preference for the *Heliothis* system because *Pieris* females do not avoid ovipositing on occupied or signaling plants. When herbivores limit their oviposition to only NE plants, the signal relevance to the parasitoids decreases (Fig. 4). By avoiding signaling plants, herbivores are increasing the proportion of SE plants relative to SO plants, so parasitoids following signals are more likely to waste time encountering empty plants. When multiple ovipositions per plant are allowed, signaling empty plants can be occupied before the entire relaxation period is complete, and thus, the signal created by the previous herbivore can still be an indicator of

the current herbivore. The impact of this behavior depends on the density of signaling plants in the field. At very low densities, limiting oviposition does not greatly decrease signal relevance because the probability of a moth laying multiple eggs on the same plant is low, so there is not much difference in field distribution for the limited or multiple oviposition conditions. At higher densities, *Rel* for multiple oviposition is greater than for the limited oviposition case because more plants can be reinfested before the signal turns off. When herbivores limit their oviposition, it narrows the density range where parasitoids benefit from following signals.



**Fig. 4** The relationship between mortality rate, host oviposition, and signal relevance. Parameters were set for *H. virescens*; plant induction and relaxation delays were both set at 5 d. In the legend, “high” and “low” refer to the high and low mortality values on Table 2, “multiple” and “limited” refer to whether a plant could be infested multiple times or if new host infestations were limited to only non-signaling, empty (NE) plants

**Host-Stage Attack Preference** As alluded to above, host-stage attack preference can interact with other parameters to decrease signal relevance. Specifically, when the parasitoid was limited to a host stage that was shorter than the induction period, the signal relevance decreased. For example, a parasitoid that could attack only first-instar *P. rapae* would have a  $Rel > 1$  if the host-plant induced after 1 or 2 d but  $Rel < 1$  if host plant induction took longer than 3 d (Fig. 3c). In the case of higher induction delays and a parasitoid limited to first instars, the SO state occurred only if the plant was reinfested with a new larva, while an older larva induced the signal, which happened at a greater frequency with high occupation rates. In this limited case,  $Rel$  increases as occupation rate increases, but it never is greater than one.

## Discussion

Parasitoid foraging in response to herbivore-induced plant volatiles is a complex behavior, and it will take a combination of multiple models that focus on different aspects of the same system to understand fully this phenomenon. Models that focus on how parasitoids forage in the micro-habitat of the plant canopy (such as Vos and Hemerik 2003) complement this model’s approach of looking at parasitoid foraging across an agricultural field. Results from this model identify several biological parameters that should be more thoroughly studied empirically.

First, the relationship between herbivore density, plant volatile production, and parasitoid response has traditionally been studied at the single-plant level. However, in this model, field-level herbivore density was shown to affect the relevance of plant volatile signals when the same quality of volatiles was produced by all signaling plants. This indicates that to understand the value of a plant’s volatiles to a foraging parasitoid, herbivore population dynamics at the landscape spatial scale must be considered.

The second point is that a delay in the initiation or cessation of volatile signal production may, in certain conditions, decrease signal relevance for a foraging parasitoid. It is not enough to measure simply whether volatiles are produced and whether parasitoids can respond physically to the cue. It is also important to ask if these volatiles are being produced in a time frame relevant to the parasitoid’s foraging behavior. This assessment should include relevant physiological constraints on the parasitoid, such as which instars are viable hosts.

The possibility has been raised in several papers of breeding for “calling” plants to enhance biological control (Takabayashi and Dicke 1996; Dicke et al. 2003). In a few studies, it has been found that parasitoids respond more strongly to some cultivars or genotypes within a plant species, indicating that genes for the volatile cues may have inadvertently been bred out of other cultivars (Fritzsch Hoballah et al. 2002; Lou et al. 2006). Part of this discrimination may be due to the specific chemicals that comprise the plants’ volatile cues. These preferences may have developed because certain plant–host complexes produce more relevant signals than others.

In addition to examining the presence or absence of volatile signal production in plants, it may be important for plant breeders to look at the relevance of signal production by plants to the parasitoids and predators of interest. A plant volatile that is useful in one geographical region may be useless in another area that has a different insect community. For example, in regions where the main parasitoid is *Cotesia rubecula*, which can successfully attack *P. rapae* in later instars, plants with later volatile releases can still manipulate the third trophic level. However, in geographic areas where the main parasitoid is *C. glomerata*, which can only attack the first two instars of *P. rapae*, the same plants will produce volatiles that are irrelevant to the third trophic level. Additionally, in some geographic regions, the presence of potential parasitoid hosts may overlap with herbivores that are non-hosts but that also trigger plants to produce volatile signals. If these volatiles are not unique for host herbivore, there may be a disproportionate number of signaling but empty (SE) plants induced by the non-host, resulting in irrelevant signals. While past emphasis has been placed on the ability to breed plants that are capable of turning on signals, it may be as

important to focus on breeding plants that can also quickly cease signaling when herbivory ceases. Within the scenarios examined with our model, we found that the greatest increase in parasitoid attack rate due to the presence of signals was fourfold. Plant breeders must therefore determine if less than a fourfold increase in attack rate will lead to economic and environmental gains substantial enough to justify a complex breeding program.

How signal relevance impacts a parasitoid species depends on their plasticity of response. Parasitoids have shown both inherent (Fritzsche Hoballah et al. 2002) and learned ability (Dicke 1999; Fukushima et al. 2002) to follow plant-produced volatile cues. A parasitoid that can learn may adjust its foraging strategy among days or even within one foraging bout based on the relevance of the signal. For a parasitoid with inherent preferences, signal relevance is more likely to act on an evolutionary timescale.

There are many possible ecological pathways through which herbivore-induced plant volatiles could affect parasitoid attack rates. We chose to focus on bypassing non-signaling plants, but there are other processes that may be at work. By altering the assumptions we made in this study, modelers can address some of these other differences. We assumed that the spatial unit of induction was a plant. Some plants begin producing volatiles when nearby plants are induced to create neighborhood effects (Karban 2001). We did not include this type of interaction, but we can speculate that this would have an effect of increasing the signaling empty (SE) plants and may also impact the area of discovery,  $a$ , if parasitoids increase their time spent foraging in signal-rich areas. If a parasitoid approaches a field and the overall volatile cloud causes it to fly slower and increase its turning radius, then this impacts the number of plants the parasitoid can land on over time ( $a_{\text{Sig}} \leq a_{\text{Ran}}$ ).

We assume that the field in which the parasitoid forages is sufficiently large so that the parasitoid will run out of time before it runs out of available hosts. The number of signaling plants in a field must be less than or equal to the total number of plants in the field, so a parasitoid's relevant environment is smaller if it is restricted to signaling plants. If a parasitoid is capable of exhausting all the hosts in its environment, we can assume it will leave the field. If then we assume that a parasitoid leaving one field will simply fly to another field with similar characteristics and continue foraging until the total time has expired, then there is no change to the variables. However, once abandoning one field, if the time it takes to reach another field is considerable or a high risk of death during transit occurs, this can effectively reduce the total time the parasitoid has available for foraging. Thus,  $T_{\text{tSig}} \leq T_{\text{tRan}}$  in all cases where hosts are a limiting factor and fields are isolated.

We assumed that handling time was constant regardless of host-plant volatiles. If handling time increases on

signaling plants where the parasitoid has a positive oviposition experience, as would occur when the parasitoid spends extra time learning the cues of a plant after a successful oviposition, then this could lead to a difference in handling time for signaling and random plants ( $b_{\text{Sig}} > b_{\text{Ran}}$ ).

Because plants were categorized by their youngest infesting larvae, cases where the youngest larva dies first were misclassified. This biases the model toward empty plants in the multiple occupation scenarios because there is higher mortality for first instar larvae, especially in the case of *H. virescens*. This bias is especially troublesome at the higher occupation rates where multiple occupation is more likely to occur. This shortcoming is addressed in the following companion paper (Puente et al. 2008) that reports results with a spatially explicit model that follows the fate of multiple larvae on a single plant. The value of this general model lies in its attempt to capture various interactions brought about by behaviors of all three trophic levels, and its ability to produce system-specific predictions.

The oviposition behavior of *H. virescens* poses a challenge to foraging parasitoids. If *H. virescens* limits oviposition to uninfested plants, the signal relevance that plants provide to parasitoids at high herbivore densities is reduced. However, as long as the density of herbivores remains low, the model predicts that parasitoids will benefit from following plant signals.

Additionally, we looked at two different life tables for *H. virescens* and found that, at low herbivore densities, plant volatiles were more relevant when mortality was high. This indicates that using other pest control methods to suppress the population produces conditions where plant signals are more relevant to parasitoids for biological control. This model supports the notion that complementary methods of pest control are better than relying on a single method such as biological control.

Because *C. glomerata* has a narrow range of host stages, we were curious to see if that would make signals less relevant. As long as *C. glomerata* is able to successfully attack second instars, following plant signals is the preferred strategy for the entire range of parameters we tested for *P. rapae*. However, when parasitoids are limited to just the first instar, they would be better off randomly foraging than following plants that take longer than 2 d to induce signals. We can predict that it would be detrimental for *C. glomerata* to follow plant signals that are not induced until larvae reach the third instar because *C. glomerata* specifically forages on the first two instars. However, in systems where it has been measured, plants responded to herbivory with volatile production well before the third instar would have been reached (Geervliet et al. 1998; Mattiacci et al. 2001; Scascighini et al. 2005).

The general deterministic model presented here quantifies the potential impact of a number of ecological factors

on the importance of induced volatiles to parasitoids. As the first biologically based model of this general system, it brings forth more questions than it answers. More detailed models tailored to specific tritrophic systems and more detailed experimental data on those systems will be needed to answer these questions.

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