ABSTRACT

PUENTE, MOLLY ELIZABETH. Synchrony of Herbivore Presence, Induced Plant Volatiles, and Parasitoid Response. (Under the direction of Fred Gould and George Kennedy.)

It has been shown in numerous systems that parasitoids are attracted to chemical volatiles produced by herbivore-damaged plants. It has been suggested that by artificially manipulating these volatiles in crop plants, biological control can be enhanced in agricultural systems. Before this technology is implemented, it is important to understand the tritrophic dynamics of the system. I used two different modeling approaches to address this phenomenon.

In the first model, I combined a modified predator-prey functional response equation with an age-structured herbivore population model. I looked at the effects of plant induction delay, plant relaxation delay, herbivore density, and parasitoid host-age preference. Parasitoids following signals had an advantage over randomly foraging parasitoids under the majority of the parameter combinations I examined, with the largest advantage occurring when plants were able to induce within one day of herbivory onset and relax signal production within one day of herbivore removal, when less than 10% of the plants were occupied by herbivores, and when parasitoids were able to attack all feeding instars of their hosts. Under most cases, higher herbivore density had a negative effect, induction delay had no noticeable effect, and shorter relaxation delays had a positive effect on signal relevance to the parasitoid. In cases where parasitoids could only attack first instar hosts, plants with an induction delay longer than two days produced signals that were irrelevant to the parasitoids,

and this loss of signal relevance worsened with shorter relaxation delays and smaller herbivore densities.

In the second model, I took a spatially-explicit stochastic simulation approach and examined the *Brassica oleraceae, Pieris rapae,* and *Cotesia rubecula* system in more detail. In addition to the variables I considered for the first model, I also looked at a parasitoid distance bias variable. Instead of varying herbivore density over a large range of parameters, I used realistic *Pieris rapae* dynamics, following three generations of herbivores (a single field season) per simulation. Similar to the previous model, parasitoids gained the most from signals when all herbivore instars were viable hosts, herbivore density was low, and relaxation delays were short. Unlike the general deterministic model, shorter induction delays could lead to considerable gains for the parasitoids in this model.

Together, the models indicate that there are some conditions that favor parasitoids following herbivore-induced plant volatiles, especially when herbivore densities are low, and plant can induce or relax their signal within a day of changes in herbivory. By creating plants that do produce signals in the right time frame, it may be possible to optimize biological control in agriculture. However, it is also apparent from my models, that herbivore-induced volatiles are ineffective during herbivore outbreak conditions, indicating that biological control alone would not be able to contain pest populations because parasitoids are limited by factors other the time it takes to find hosts, which is the primary way herbivore-induced plant volatiles can aid foraging parasitoids.

Improving biological control is one of the practices growers can adopt as part of Integrated Pest Management (IPM), and in the final section of this dissertation I discussed the results of a survey exploring how growers adopt IPM. I found that practices consistent

with IPM were adopted in a piecemeal fashion by cotton growers in the eastern part of the state. My analysis indicated that growers did not see all these practices as part of a single management decision, but rather as parts of many independent decisions, dealing with weed management, insect management, crop management, and ecosystem management.

SYNCHRONY OF HERBIVORE PRESENCE, INDUCED PLANT VOLATILES, AND PARASTOID RESPONSE

by

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DEDICATION

This dissertation is dedicated to the women of the Puente-Palm family.

For Dr. Sally Palm, who was my inspiration for studying biology. As a child, I looked up to Aunt Sally to have all the right answers on everything ranging from toasting marshmallows and identifying plants to diagnosing illnesses and fixing machines. I knew from a young age that I also had to get a doctorate in science, just so that I could know everything just like Aunt Sally.

For Emily Puente, who has been the most patient and caring sister a girl could ever want. She couldn't care less about entomology, but she never held it against me when I hung up on her because I was stressed from research or in the middle of writing a paper. She reminded me that it was okay to take a break and relax every once in a while. I thank her for reminding me that even if life is a rat race, it doesn't mean you have to spend your entire time running.

And lastly, for Linda Puente, who always wanted to be a scientist and never got the chance. When I was desperate for insects for my ENT 502 collection, she went out catching butterflies in her cast and stored beetles in her freezer for me. She's been there for me when my field seasons fell apart, when my computer crashed, and for all the other bumps along the road of this degree. She's been the best roommate a graduate student could hope for. Here's to you, Mom!

BIOGRAPHY

Molly Puente was born May 27, 1979, in Minneapolis, MN. She went to kindergarten in Aurora, CO, attended primary school in Urbandale, IA, and attended high school in The Woodlands, TX. From 1992 to 1995, she attended the Duke University TIP program, including four summers spent at Duke University and a spring trip to Costa Rica. She graduated from The John Cooper School in 1997.

Having developed a love of Duke from her summer camp experiences, it's no surprise she matriculated there in 1997, and rapidly became active in campus activities. Molly was a member of the Science and Society FOCUS group, played violin in the Duke University Orchestra, held numerous offices in the Arts Theme House, and became a sister in Alpha Epsilon Phi sorority. During the summers she worked in the biology department with Nora Underwood, Kristi Westover, and Bill Morris on several projects. When lab work was light, Nora would encourage Molly to catch insects from their field site and key them out for fun. In this way, Molly started her first insect collection and discovered the exciting world of entomology. In 2001, Molly graduated with a B.S. degree in biology.

Following Duke, Molly immediately began her doctorate program at N.C. State University, sponsored by a Keck Center for Behavioral Biology Fellowship and a National Science Foundation Fellowship. Three years into her doctorate, Molly's interests shifted towards science policy. In 2006, Molly completed a Masters in Public Administration from NC State University.

Her dissertation on the "Synchrony of Herbivore Presence, Induced Plant Volatiles, and Parasitoid Response" was advised by Drs. Fred Gould and George Kennedy.

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CHAPTER I

LITERATURE REVIEW OF TRITROPHIC RESPONSES TO HERBIVORY

Introduction

Insect predators and parasitoids play a pivotal role in many ecosystems and are economically important as biological controls of pest species. The effectiveness of a predator depends on where it decides to forage and how long it occupies any one patch (Charnov 1976). While the Marginal Value Theory and the various tests of this theory (e.g. Driessen et al. 1995, Tenhumberg et al. 2001, Wajnberg et al. 2000, Pierre et al. 2003) have tackled the second question, there is a limited body of observations and no explicit models dealing with that first question of how a predator decides which patch to visit. Understanding the constraints on natural enemy attraction is important in the context of biological control (Beddington et al. 1978, Lewis and Martin 1990, Degenhardt et al. 2003).

One major constraint for predators can be described as the reliability/detectability problem (Vet and Dicke 1992). Predators search for their prey at the same time the prey are under evolutionary pressure not to be found. The most reliable cues for the prey would originate from the prey themselves, but this is under selection to be undetectable (Jeffries and Lawton 1984). Predators instead can resort to cues from the prey's host plant as a proxy for the prey, but conversely these cues are often unreliable indicators of the prey's location. Foraging predators and parasitoids face a trade-off; either they can follow cues that are reliable but under selection to be undetectable, or they can follow cues that are readily detectable but less specific and therefore less reliable host indicators.

When plants are wounded, such as by herbivores, they often produce chemical volatiles through the jasmonic acid pathway (Constabel and Ryan 1998, Cipollini and Redman 1999). It has been suggested that inducible plant volatiles allow the predators to get around this problem by providing a detectable cue that is also a reliable indicator (Vet et al.

1991). In fact, it has been shown in numerous systems that natural enemies are both inherently attracted to host-plant cues (Lewis and Martin 1990, Wang et al. 2004) and can learn to respond to host-plant cues (Lewis and Martin 1990, Kester and Barbosa 1991).

Systemic herbivore induction has been shown in numerous plant species (Dicke 1999). The impact of plant induction directly on herbivores has been identified in numerous systems (see review: Karban and Baldwin 1997). Direct defenses, both constitutive and induced, typically affect a broad spectrum of herbivores (Dicke and Takabayashi 1991), while induced defense can either have a broad affect (Karban et al. 1997) or be species specific. The tritrophic repercussions of induced plant responses are much more difficult to measure (Faeth 1992). Attracting natural enemies has been shown to increase plant fitness in some situations (Gomez and Zamora 1994, Degenhardt et al. 2003, Fritzsche Hoballah and Turlings 2001) while lowering plant fitness in others (Janssen et al. 2002, Coleman et al. 1999). Similarly, in some systems, herbivore populations are significantly reduced by parasitoids responding to plant cues (Thaler 1999, Liu and Jiang 2003, Degenhardt et al. 2003) while in other cases, the herbivore populations are unaffected by the natural enemy response. Finally, the long term fitness benefits of responding to host cues has not been calculated for most natural enemies.

Creating an environment that maximizes natural enemy effectiveness would aid organic growers who rely heavily on natural enemies. However, artificially enhancing the environment with attractive cues may backfire if the cues interfere in predator learning or perception (Powell 1986, Lewis 1992, Dicke et al. 1990). Before introducing any sort of trait that depends on tritrophic interactions, a careful study of the costs and benefits should be conducted (Poppy and Sutherland 2004). The costs and benefits of herbivore induced plant

volatiles are particularly difficult to study in real field situations because the evolutionary history of the organisms is tangled with the current functioning of the system. Additionally, it is often difficult to disentangle the mechanism of natural enemy response in field situations (Gross 1981). For example, while it has been demonstrated that natural enemy populations are greater in fields that have been augmented with jasmonic acid or methyl salicylate (Thaler 1999, James and Price 2004), it is unclear whether this is a case of attraction over distances or retention of the population already present.

The purpose of this paper is to review many of the systems currently being studied as examples of induction. An earlier review by Takabayashi and Dicke (1996) identified >15 plant species, >10 herbivore species, and >10 predator species that have shown characteristics of a tritrophically induced system. This review includes several of these systems, and others, in hopes of organizing what is known about signal reliability. As identified by van der Meijden and Klinkhamer (2000), there are several conditions that are necessary to determine that herbivore-induced plant volatiles were indeed evolved as a plant defense mechanism. These include a proper abundance of natural enemies, a reliable cue, a locally specific cue, and a fitness benefit to the plants by increasing natural enemies. While the review will try to highlight these four conditions, the special emphasis will be on signal reliability and local specificity. Additionally, this paper will identify where modeling may be appropriate for filling in the unknown parameters that impact these conditions in currently studied systems.

Ecological modeling is a useful method for tackling systems where there are many gaps in basic knowledge and to put these case studies in a broader context (May and Hassell 1988). Modeling allows a wider range of parameters to be tested, so it can be determined

which parameters are not found in nature by chance versus by active selection against those parameters. This is especially crucial in this area of study where many of the model systems have been under agricultural selection for traits such as yield rather than natural selection for traits such as volatile production. Additionally, models may be able to link empirical observations of individual behaviors to predictions about population dynamics. While a large literature exists on the behavior of various parasitoid-host-plant systems, there is a lack of models in this area that can link the behavior back to population ecology (Vet 2001).

Egg Parasitoids

Because eggs do not cause direct herbivory damage, information on egg parasitoid reaction to induced plant volatiles is scarce. However, there are several examples of egg parasitoids being able to orient to host species' derived cues and related plant cues (e.g. Noldus et al. 1991). Infochemical detour is the process of using cues from alternate host stages as proxies for the intended host stage (Vet and Dicke 1992), and may provide egg and pupal parasitoids with a mechanism for using induced plant volatiles.

In one of the few tritrophic egg induction systems known, it was found that the egg parasitoid *Oomyzus gallerucae* could be attracted to volatiles from *Ulmus minor* following oviposition by *Xanthogaleruca luteola*, the elm leaf beetle. This signal was shown to be highly localized, and triggered by the jasmonic acid pathway (Wegener et al. 2001). Analysis of headspace volatiles showed that the signal from ovipositing damage overlapped with the signal from herbivory, and that jasmonic acid induction from feeding could elicit the same terpenes as natural oviposition, but lacked the sesquiterpenes found in volatiles from oviposition damage. Because parasitoids were equally attracted to jasmonic acid treatments

as natural oviposition damage, it is likely that the terpenes play a much larger role in signaling to parasitoids than the sesquiterpenes.

Jasmonic acid (JA) was also indicated in the elicitation of terpenes of *Pinus sylvestri* twigs damaged by oviposition by the sawfly *Diprion pini* (Mumm et al., 2003). After finding that the parasitoid *Chrysonotomyia ruforum* was preferentially attracted to ovipositor-damaged twigs rather than mechanically damaged twigs, headspace volatiles were collected from ovipositor damaged twigs, mechanically damaged twigs, and JA-treated mechanically damaged twigs. The higher quantity of (E)-β-farnesene in both oviposited and JA-treated twigs makes it a likely candidate for the signal that cues C. ruforum of a host's presence.

It is possible for *Trichogramma brassicae* to utilize plant cues when foraging, preferentially searching for *Helicoverpa punctigera* eggs on the host plant to which they were exposed at emergence. There was a strain effect, with one *T. brassicae* strain much more likely to search on tomato plants for longer periods if having previously experienced tomato, while another strain showed no effect of emergence environment (Bjorksten and Hoffman 1998). Emerging on lettuce did not affect *T. brassicae* foraging patterns. In another example, *T. brassicae* was shown to have positive arrestment behaviors to leaf discs from Brussels sprouts (*Brassica oleraceae*) plants that had been exposed to *Pieris brassicae*. The discs were most arresting 72 hours after the eggs had been laid, indicating a systemic induction in the plant as opposed to residual host cues from the butterflies, which were present at the 12 and 24 hour marks (Fatouros et al. 2005a). This time course is especially interesting as *Trichogramma* females preferentially oviposit in eggs 72 hours old.

The egg parasitoid *Tissolcus basalis* (Wollaston) was shown to respond to cues from its host pentatomid, *Nezara viridula*. In a Y-tube olfactometer, *T. basalis* was attracted to

odors from adult, pre-ovipositional female *N. viridula*, but not other *N. viridula*. Contact cues were tested in petri dish arena assays, where *T. basalis* responded with arrestment behavior when presented cues of pre-ovipositional females, but not cues from males or virgin females (Colazza et al. 1999). While this shows considerable host specificity for the parasitoid, this study did not include a third trophic level.

It was found that *Lygus hesperus* females can induce cotton to release systemic, volatile terpenes by rupturing cells with her ovipositor (Rodriguez-Saona et al. 2002). However, there was no indication that egg parasitoids took advantage of this plant derived cue of egg presence.

These studies indicate that the act of oviposition by herbivores is sufficient in some cases for a plant to produce induced volatiles. In all known cases, induced volatiles are only present if the ovipositing adult physically damages the plant (Hilker et al. 2005). Egg parasitism should always increase plant fitness because it prevents the herbivore from ever hatching to damage the plant (Hilker et al. 2005). Therefore, although we do not have many known examples to date, it is likely that selection pressure for attracting parasitoids of destructive pests will be high for plants.

A major shortfall of these studies is that the spatial scale of attraction is unknown. Field studies did not indicate the distance that insects were attracted from, and laboratory studies operate on very small spatial scales. Also with the exception of the *Brassica* system, the time course of plant induction has not been explored. For example, the *Pinus sylvestris* studies have only looked at plant volatile production 72 hours after damage (Hilker et al. 2005), but it is not clear if eggs that old are still viable hosts for the parasitoids. Also, if

volatiles continue to be produced after the eggs have hatched, the reliability of these signals may decrease for egg parasitoids, but there is no indication that this has been studied.

Lepidopteran Larval Parasitoids

There is a considerable literature on the parasitoids of Lepidopteran larvae because many caterpillars are important crop pests. Parasitoids are often more host specific than predators, making them more ideal candidates for biological control programs. This, along with the fact that a single host encounter generally results in a single parasitoid offspring, makes them a popular subject for predator-prey models (Lawton et al. 1975).

Campoletis sonorensis (Cameron) (Ichneumonidae) uses *Heliothis virescens* as a common host. Baehrecke et al. (1990) looked at the possible interaction of *Gossypium hirsutum* (cotton), a host for *H. virescens*, on the foraging activity of *C. sonorensis*. In a wind tunnel, naive *C. sonorensis* adults were watched for four minutes and allowed to fly towards the following treatments: undamaged cotton, mechanically damaged cotton, host-plant complex, and herbivore induced cotton with herbivore removed. After landing, wasps were allowed to forage on the plants for two minutes. Wasps tended to spend more time on the damaged plants, but showed no preference for volatile differences. One possible explanation is that *Campoletis sonorensis* responds to visual cues rather than olfactory cues. Having a damaged plant visibly available was shown to increase positive flight responses in wind tunnel assays (McAuslane et al., 1991). In the same set of experiments, there was no difference shown in attraction between mechanically and naturally damaged cotton, but damage of any type was more attractive than undamaged plants.

Cardiochiles nigriceps also uses *Heliothis virescens* as a host. *H. virescens* shares many of its host plants with *Helicoverpa zea*, including tobacco and cotton, but *Cardiochiles*

nigriceps does not use *H. zea* as a host. De Moraes et al. (1998) showed that in the field, *C. nigriceps* visited tobacco and cotton plants more readily when they were infested with *H. virescens* than *H. zea* or mechanically damaged. In a different field experiment, *Cardiochiles nigriceps* was shown to prefer *H. virescens* damaged tobacco over *H. virescens* damaged cotton, regardless of the background volatiles (cotton field or tobacco field) (De Moraes and Lewis 1999). Capturing head space volatiles after 24-48 hours of feeding, showed that tobacco, cotton, and corn all produce unique volatile signatures for *H. virescens* and *H. zea*, giving the parasitoids the cues they need to differentiate between hosts (De Moraes et al. 1998).

In addition to sharing host plants, *H. virescens* and *H. zea* also share the parasitoid, *Microplitis croci*epes. In wind tunnel experiments, *M. croceipes* preferred *H. virescens* damaged cotton, regardless of what host-plant it experienced with training flights to *H. virescens*. However, when given a choice between *H. virescens* and *H. zea* induced plants, *M. croceipes* made no choice (De Moraes and Lewis 1999). It appears that *M. croceipes* can distinguish herbivore induced plant volatiles from non-herbivore induced plants (Rose et al. 1998), but does not draw a distinction of what herbivore is inducing that plant. It has been suggested this is to reduce competition with *Cardiochiles nigriceps* which prefers *H. virescens*-induced tobacco over cotton in the field (Oppenheim and Gould 2002).

M. croceipes might in fact be more attracted to innate cotton volatiles rather than herbivore induced plant volatiles. In another experiment with *Microplitis croceipes*, *Heliothis virescens*, and cotton, it was found that in wind tunnels, *M. croceipes* was attracted to cotton volatiles, even if the cotton was not induced by *H. virescens*, and that this was increased by including *H. virescens* frass (Elzen et al. 1987). *Campoletis sonorensis*, another generalist

parasitoid that can attack *H. virescens* on a variety of host plants, was also found to be attracted to uninduced cotton, and adding frass from *H. virescens* did nothing to increase the attraction (Elzen et al. 1987).

M. croceipes was also compared to the generalist parasitoid *Cotesia marginiventris*. In wind tunnel experiments both parasitoids were attracted to cotton volatiles damaged by *Spodoptera exigua* over undamaged plants. Surprisingly, the generalist *C. marginiventris* showed a much stronger attraction to induced plant volatiles, especially when induced by *S. exigua*, while the specialist *M. croceipes* responded to both *S. exigua* and *H. zea* damage equally (Cortesero et al., 1997). No explanation was given for this difference in levels of attraction.

The elicited signals in *Zea mays*, brought on by *Spodoptera* damage, has been one of the most well studied chemical pathways of induction. Turlings et al. (1992) found that two hours of beet armyworm (*Spodoptera exigua*) feeding induced corn seedlings to systemically produce terpenoids 15 hours later. This terpenoid production could be simulated by mechanically damaging the plants and then applying larval regurgitant, but not by superficially applying regurgitant or by sharing airspace with a damaged seedling. Plants producing terpenoids were shown to be attractive to *Cotesia marginiventris* in wind tunnel experiments (Turlings et al. 1992).

In a more detailed examination of the system, Fritzsche Hoballah et al. (2002) looked at headspace volatiles in eight different corn varieties and cowpea (*Vigna unguiculata*) when induced by *Spodoptera littoralis*. While there was a wide variation in produced volatiles, in Y-tube olfactometer assays, *Cotesia marginiventris* showed no preference between most combinations of corn varieties. Wasps preferred cowpea, which had the most general

composition (high in green leaf volatiles) of the options. There was some indication that wasps preferred the plants that produced the greatest quantity of volatiles regardless of composition. Another study looking at the variability in *Zea mays* subspecies and *Zea spp*. (teosinte) found that *Spodoptera littoralis* regurgitant could induce a wide variety of compounds and quantities of compounds in very closely related plants (Gouinguene et al. 2001). Additionally, different strains showed different quantities of volatiles emitted over different time courses, some rising steadily up to 16 hours after damage, while others peaked at about 12 hours following damage. None of the tested cultivars showed the highest amount of volatiles at the earliest time period (7-10 hours following induction.) (Gouinguene et al. 2001) Clearly there is a delay between herbivore presence and volatile production, but it remains to be seen whether this impacts the relevance of the signal to the parasitoids.

In addition to production delays, there is also the possibility of plants being elicited by nonsusceptible instars. The parasitoid, *Microplitis rufiventris*, is able to parasitize only second and third instars of *S. littoralis*, but in olfactometer experiments, the wasp responded to second, third, and fifth instar induced plants over undamaged plants. Even when the wasps were given oviposition experience on seconds and thirds, they showed no preference for younger instars in wind tunnel experiments (Gouinguene et al. 2003). In chemical assays, the suspected elicitor was found in the regurgitant of all instar ages, and the headspace volatiles were not significantly different in composition between different aged inducers (Gouinguene et al. 2003). This means that wasps responding to the induced signal in nature must make the mistake of finding larvae that are too old to be parasitized.

The consequences of attracting parasitoids, from the plant's point of view, were shown to be significant in the case of *Zea mays* attacked by *Spodoptera littoralis*. Plants were

infested with either healthy larvae or larvae parasitized by *Cotesia marginiventris*. Plants with parasitized larvae showed no significant difference from controls, but significant difference from plants infested with non-parasitized larvae, in terms of number of ears, number of seeds, and seed weight, indicating a benefit from attracting parasitoids (Fritzsche Hoballah and Turlings 2001). *S. littoralis* larvae both gained less weight and stopped feeding earlier than healthy larvae when parasitized by *Cotesia marginiventris* or *Campoletis sonorensis* (Fritzsche Hoballah and Turlings 2001).

The Braconid wasp, *Cotesia kariyai* Watanabe, parasitizes the common armyworm, *Mythimna separata* (Walker) larvae from second to sixth instars. It is commonly used as a biological control agent on armyworm in grain crops in Asian tropical and temperate zones. Fukushima et al. (2002) tested naïve and conditioned wasps' response to three different synthetic blends. The first blend was composed of volatiles found in corn head space when being induced by armyworms. The second blend was composed of volatiles found in non-induced corn; and the third was a mix of the previous two. All blends were composed of synthetically derived chemicals absorbed in filter paper, but they performed as well as full leaves in the assay setup. The assay consisted of counting whether female wasps landed on a target or not in a five minute period when flown in a wind tunnel. It was found that conditioned wasps had a significantly greater landing rate for all blends, but especially the mixed blend. The naïve wasps had more successful landings on the mixed blend, followed by the induced blend, indicating that they do have an innate response to induced odors, but that augmenting that odor with a complete plant profile increases the wasp's ability to identify the plant.

A related parasitoid, *Cotesia plutellae*, specializes on *Plutella xlyostella*, the diamondback moth. Multiple *P. xylostella* larvae can develop on cabbage plants, and it was found that moths will preferentially oviposit on plants that have conspecific larvae present (Shiojiri and Takabayashi 2003). In cages, naïve mated *C. plutellae* showed no preference towards plants that had been heavily infested (30 larvae/plant for 24 hours before assay) over plants that had been less heavily infested (10 larvae/plant for 24 hours before assay) (Shiojiri and Takabayashi 2003). In the same study it was found that wasps oviposited in less than two larvae per plant, even at the high infestation levels. This was seen as an example of the "encounter-dilution effect" where moths took advantage of the wasp's constant attack per plant rate by aggregating their offspring.

Perhaps this oviposition control contributed to the results found in Karimzadeh et al. (2004), where they tracked the long term population sizes of *C. plutellae* and *P. xylostella* given a fixed resource of either *Brassica rapa* or *Brassica napus*. While short term data indicated that *C. plutellae* preferred larvae on *B. napus*, and that *P. xylostella* developed more slowly on *B. napus*, the equilibrium populations were not significantly different on either host plant, raising the question of whether parasitoid efficiency actually matters in the long run for plant-herbivore systems.

While *P. xylostella* is capable of feeding on multiple host plants, including the cabbage species *Brassica oleracea*, it was found that *Cotesia plutellae* responds preferentially to Chinese cabbage, *Brassica campestris*, over cabbage (Liu and Jiang 2003). In a caged experiment, more larvae were parasitized on Chinese cabbage than regular cabbage; however, by giving wasps experience on regular cabbage, the preference shifted. This was then shown, through a series of y-tube olfactometer assays on both cabbage species,

to be due to herbivore induced volatiles. Interestingly, plants where larvae had been removed before the assay were just as attractive as actively infested plants indicating a delay in the plant's ability to turn off volatile production (Liu and Jiang 2003).

Another parasitoid of *P. xylostella*, *Diadegma semiclausum*, showed a similar preference. Wasps spent the same time searching cabbage plants that had larvae actively feeding as they spent on plants on which the larvae had fed for 24 hours and then been removed before the plants were placed in the wind tunnel; both of these treatments were searched significantly longer than plants that had never had larvae on them (Wang and Keller 2004). Additionally it was found that *D. semiclausum* was more likely to stay longer on plants with larvae that had been parasitized by *Cotesia plutellae*, than on plants that had larvae that were unparasitized or parasitized by *D. semiclausum* (Wang and Keller 2004).

It was found that cabbage does not induce a direct defense against *Pieris brassicae*, so researchers suspect this plant is likely to produce an indirect induced defense (Coleman et al. 1999). The parasitoid *Cotesia glomerata* was found to respond to *Pieris rapae*- induced Brussels sprouts (*Brassica oleracea*) (Geervliet et al. 1994). The Brussels sprouts produce an increased level of green leaf volatiles when exposed to *Pieris brassicae* saliva, either through caterpillar feeding or through artificially applying saliva (Mattiacci et al. 1994). Interestingly, it was found that there was a minimum density of *P. rapae* needed before volatiles were emitted (Geervliet et al. 1998). Both *Cotesia glomerata* and *Cotesia rubecula* were shown to respond to high densities of *Pieris brassica* and *Pieris rapae*, respectively, on plants in a wind tunnel (Kaiser and Cardé 1992, Nealis 1990). The effect of density was so important, that both *Cotesia* species would fly to the odor source with the highest density of larvae even if the plant/herbivore combination was not the correct host for the parasitoid (Geervliet et al.

1998). Agelopoulos and Keller (1994) showed that *Cotesia rubecula*, when given a choice between cabbage plants infested with their host *Pieris rapae* or plants infested with the non-host *Plutella xylostella*, would fly to the downwind plant, indicating a preference for quantity of volatiles over specificity of volatiles. This dependence on volatile density may explain why *Cotesia rubecula* is more responsive to the more abundant damaged host plant volatiles than the more specific volatiles from host feces (Agelopoulos et al. 1995). The dependence on plant volatile density translated to a three day lag between the beginning of herbivore damage and the wasp's response, and a one day lag between the cessation of herbivore feeding and the ending of wasp discrimination in wind tunnel assays (Mattiacci et al. 2001). Mattiacci et al. (2001) is one of the few studies that actually examined the time course of induction, and the presence of time lag is important to note.

Additionally, in these systems, it was found that the parasitoids could distinguish between plants that hosted parasitized versus unparasitized larvae using plant volatile cues (Fatouros et al. 2005b). This is an especially important finding for *Cotesia rubecula*, because only the oldest parasitoid larva typically survives superparasitism. At close range, *C. rubecula* preferentially are attracted to host feces from second instar individuals over fourth instar individuals (Agelopoulos et al. 1995). However, from a distance, *Cotesia rubecula* was more attracted to plant damage caused by older larvae, probably due to the relative amount of damage larger larvae can cause (Nealis 1990).

However, there are some unresolved questions with the *Cotesia-Pieris-Brassica* systems. *Cotesia glomerata* primarily attacks the first and second instars of *Pieris brassicae*, but cannot distinguish earlier instars from later instars by herbivore induced plant volatiles on Brussel sprouts (Mattiacci and Dicke 1995). It was also shown that parasitism by *C.*

glomerata did not reduce the amount of plant material a larva consumed, thus would not provide protection for a plant, even if successfully signaled (Coleman et al. 1999). While these findings question the utility of this study system, it is possible that these experiments did not accurately account for density effects or multigenerational effects.

Also of note is that *C. glomerata* preferentially parasitized *P. rapae* that were sharing a plant with *Plutella xylostella* over plants that just had *P. rapae* feeding (Shiojiri et al. 2002). This was not reciprocated; *C. plutellae* preferentially parasitized *P. xylostella* that did not share plants with *P. rapae*. It was found that *P. xylostella* moths preferentially oviposited on plants that were induced by *P. rapae*, perhaps because *P. rapae* interfered with the signal *C. plutellae* used for parasitism (Shiojiri et al. 2002). This is one of the few examples of herbivores taking advantage of competitor's intereference in plant signals to predators.

In Europe, *Cotesia rubecula* is a common parasitoid of *Pieris rapae*, a generalist that attacks many important hosts, including *Arabadopsis thaliana*. Parasitized *P. rapae* consume less plant material, and do not reduce fecundity to the degree healthy larvae do, so it is in *Arabadopsis*' best interest to attract *C. rubecula* (van Loon et al. 2000). Because *Arabadopsis* is a model organism for genetics, this system can be used to look at the mechanisms behind tritrophic interactions, especially the downstream regulations that lead to species specific volatile emissions (Heil and Baldwin 2002, Dicke et al. 2003, De Vos et al. 2005). Van Poecke et al. (2001) demonstrated in wind tunnel assays that *C. rubecula* was more attracted to *A. thaliana* infested with *P. rapae* than artificially damaged or undamaged plants. Additionally, they showed that as larvae mature on plants from one to six days, the plants' attractiveness to wasps increases. Analysis of headspace volatiles showed several unique components from herbivore-induced plants, and genes in the methyl salicylate pathway were

shown to be upregulated in the presence of herbivory. However, these volatiles were not unique to *P. rapae* damage, as *C. rubecula* responded just as well in wind tunnel assays with *Plutella xylostella, Spodoptera exigua*, and *Tetranychus urticae* (van Poecke et al. 2003). Additionally, naïve *C. rubecula*'s response appears to be dependent on *P. rapae* density (Kaiser and Carde 1991), although this sensitivity appears to decline with oviposition experience.

Many studies have been done looking at the mechanisms of induction and parasitoid response in these Lepidopteran larval systems, but no one system has been able to demonstrate the fitness costs and benefis at all three trophic levels. While the time course of induction has been studied for plants damaged by *Pieris rapae* and *Spodoptera littoralis* (Mattiacci et al. 2001, Gouinguene et al. 2001, De Vos et al. 2005), these herbivores are generalists and it is unclear whether these times hold true for all host plants or just the host plants used in the experiments. Additionally, the ecological significance of these time courses has not been adequately addressed. For example, a study looking at *Arabadopsis thaliana*, found that parasitized *Pieris rapae* larvae consumed less plant material over time (van Loon et al. 2001), but another study looking at *Rorippa indica*, found that parasitized *Pieris rapae* larvae consumed more plant material over time (Horikoshi et al. 1997). Furthermore, many of the studies looking at "long-range" parasitoid attraction were done in wind tunnels of a fixed distance (e.g. Geervliet et al. 1994). The spatial scale at which volatiles are detectable and useful has not been thoroughly described for any system.

Other Parasitoids

Biological control of the cassava mealybug, *Phenacoccus herreni* (William), has received considerable interest in South America and Africa. *Aenasius vexans* Kerrich and

Apoanagyrus diversicornis are both larval parasitoids of the mealybug. In Y-tube olfactometer assays, ten minutes in duration, both parasitoids were tested for preferences of odors originating from larvae, infested leaves, induced but cleaned leaves, uninduced leaves, and controls. It was shown that both species of parasitoids were more highly attracted to damaged leaves than other treatments, including the hosts themselves (Bertschy et al. 2001).

A related cassava system of *Phenococcus manihoti* and *Apoanagyrus lopezi* showed similar results (Souissi et al., 1998). In a y-tube olfactometer study, *A. lopezi* preferred induced plant cues over all other options. Mealybugs that had been exposed to plant volatiles were attractive for the first 20 minutes, but this effect lessened after 24 hours. Also, *A. lopezi* were able to distinguish between parasitized and unparasitized hosts both on and off plants, avoiding hyperparasitism whenever possible.

The cabbage root fly, *Delia radicum*, is a major pest of several vegetables, therefore there has been interest in its parasitoids, including *Trybliographa rapae*. *T. rapae* was shown to be attracted to infested turnip roots, in olfactometer assays. In fact, not only was *T. rapae* attracted to infested roots, but also leaves and undamaged roots of infested plants, while showing no response to mechanical damage, and a repellency to uninfested roots (Neveu et al. 2002). In these tests, infestations meant larvae had been in the turnip roots for 5-7 days, and remained on the plant during the assay.

Similar to the apparency problems *T. rapae* faces with searching for root feeding *D. radicum*, the parasitoid *Dentichasmias busseolae* faces problems when looking for its host, the pupae of the stemborer *Chilo partellus*. In a y-tube olfactometer study, it was found that *D. busseolae* was attracted to the host plants sorghum and maize, while being actively repelled by the non-host molasses grass (Gohole et al. 2003). Interestingly, *D. busseolae* was

more attracted to plants infested with host larvae than non-infested plants even though larvae were not a valid host stage, lending support to the infochemical detour theory (Vet and Dicke 1992).

Pholetesor bicolor, a parasitoid of the apple leafminer *Phyllonorycter pomonella*, was more likely to probe with its ovipositor when exposed to extracts of a mine (damaged leaf epidermal tissue) than when exposed to either larvae or frass of its host (Dutton et al. 2000). In this case, the host volatiles are not acting as an attractant so much as a releaser for ovipositional behavior.

Aphidius colemani is a parasitoid of the peach potato aphid, *Myzus persicae* which attacks many species. In an olfactometer experiment it was shown that *A. colemani* innately preferred the odor of uninfested rape (*Brassica napus*) over uninfested Chinese cabbage (*Brassica chinensis*), however when the plants are infested, the parasitoid showed preference for the plant that they emerged from (Storeck et al. 2000). This example of learning induced cues from emergent experience was then complicated. When wasps were given oviposition experience before the assay, they would prefer the odor of infested plants from their positive oviposition experience above the odor of the plant they emerged from. This indicates that parasitoids of generalist species may have a great deal of plasticity when learning potential host cues.

Aphidius ervi is a parasitoid of the pea aphid *Acyrthosiphon pisum*, which infests the broad bean plant, *Vicia faba*. It has been shown that induced plants are capable of attracting *A. ervi* (Du et al., 1998). The components found in volatiles are attractive individually as well as in the induced blend, which is surprising because the components were very general ((E)-β-ocimene, 6-methy-5-hepten-2-one, linalool, geranic acid, and (E)- β-farnesene), and found

in both *Spodoptera exigua* induction and *Tetranychus urticae* induction. These components also showed considerable variation in time, with all except (E)-β-ocimene increasing at different rates over four days of exposure to aphids (Du et al., 1998). Guerrieri et al. (2002) found that not only does the damaged plant attract parasitoids, but that plants sharing soil or water, but not airspace, with damaged plants are capable of attracting *A. ervi*. This indicates an underground plant-plant signaling mechanism. While the authors claim this may create a "focus of attractiveness", benefiting the plants, it may also lower the specificity of the plant signal.

Sullivan et al. (1997) did a field study test to determine what was attractive to parasitoids of southern pine beetles (SPB). Two different species of parasitoids responded in large numbers to field trappings, one species preferring bark for late brood SPB larvae, and the other preferring bark for early brood SPB larvae. Neither showed a preference for the bole of infested trees, nor did they show an attraction to a blank control. A follow up was done comparing late bark extract with bark, synthetic bait, and a blank control. Once again late brood bark was preferred, but the extract was not significantly different (indicating that there was definitely a bark aspect to the attraction and not the host itself), and both were significantly greater than the synthetic blend which included all the same main components.

The parasitoid *Leptopilina heterotoma* must search for its *Drosophila* hosts on a variety of substrates, and thus it has been used to study the plasticity of parasitoid response. Vet et al. (1998) demonstrated that while parasitoids may be able to process many host-substrate cues, they do not discriminate between odor sources unless they are provided incentives. While other researchers have looked at "naïve" wasps learning novel cues, this system indicates that learning to ignore unprofitable cues can be just as important.

Arachnids/ Mites

The *Phytoseiulus persimilis/Tetranychus urticae* system has been studied in depth at a very small spatial scale. *Tetranychus urticae* is a generalist that feeds on hundreds of plant species. Some plant species, such as *Cucumis sativus*, have induced chemical defenses that directly impact *T. urticae* (Agrawal et al. 1999a), but there is also evidence that plant volatiles can influence the third trophic level as well. A comparative study that looked at 11 potential host species found several common volatiles were produced specifically in response to mite damage (van den Boom et al. 2004). Methyl salicylate, (E,E)-α-farnesene, and various nitrogen compounds were the most common compounds found unique to the headspace of herbivore-damaged plants. Additionally, several plants maintained the same components but changed the relative amounts or upregulated the production of the entire suite of volatiles. Different plant species responded in varying levels of volatile intensity, and there was no clear trend indicating a trade-off between direct and indirect defense. The predaceous mite, *P. persimilis* is inherently more attracted to some of these plant species' volatile blends more than others (Dicke and Takabayashi 1991). Additionally, some strains of *P. persimilis* were more attracted to plant volatile blends than other strains, indicating heritable variation in attraction (Jia et al. 2002). To add to this complexity, some strains of *Tetranychus urticae* caused a more sensitive response in host plants allowing *P. persimilis* to detect hosts at different densities depending on the host strain (Takabayashi et al. 2000).

One plant that is highly attractive to *P. persimilis* is *Phaseolus lunatus* (lima bean). In contained environments it was shown that *P. persimilis* both increased immigration and emigration when exposed to host plant volatile cues (Pels and Sabelis 2000). Additionally, *P.*

persimilis could be trained to prefer host plant species, when given a week of previous experience of *T. urticae* on either lima bean or cucumber plants (Dicke et al. 1990).

Identifying the chemical basis of the predaceous mite's arrestment has been a tricky endeavor. The octadecanoid pathway is capable of eliciting a response by *P. persimilis* to plant volatiles; however it is not as attractive as an infested lima bean plant, and headspace volatiles indicate that at least ten components of induced volatiles are due to some other pathway (Dicke et al., 1999). Additionally, four of the compounds that were identified as primary kairomone components in infested plants (4,8-Dimethyl-1,3(E),7- nonatriene, Linalool, Methyl salicylate, and (E)-β-Ocimene) were found in the headspace of uninfested and artificially damaged plants, but at much lower concentrations (Dicke et al. 1990).

Plants remain attractive to predaceous mites following removal of spider mites, but the spider mites themselves are not attractive without plant volatiles (Dicke and Takabayashi 1991). A time series study found plants most attractive two and four days following initial exposure to Jasmonic Acid, and this attraction was not evident on days 1, 7, or 14 (Dicke et al., 1999). Additionally, infested plants were able to induce plants downwind, but only after four to five days of exposure (Dicke et al., 1990).

Generalist/Omnivorous Predators

Western flower thrips (*Frankiniella occidentalis*) are omnivorous, feeding both on spider mites and plant foliage. It was found that on cotton, thrips consumed less plant material on plants that had been induced by mites (with mites removed) than on plants not induced (Agrawal et al. 1999b). When allowed access to mites on the plants, thrips consumed twice as much prey and half as much plant material on induced plants than uninduced plants. One theory is that the thrips prefer mites over plants, but that when mite resources are

limited, thrips will consume plants. By providing mite cues, the cotton plants are reducing their own damage by thrips.

In a different experiment, thrips were one of the prey items for the *predator Orius tristicolor*. *O. tristicolor* was shown to have different foraging patterns based on its perception of available hosts (*Frankliniella occidentalis* or *Tetranychus urticae*) and previous damage to *Phaseolus vulgaris* foliage (VanLaerhoven et al., 2000). In preference tests, *O. tristicolor* preferred *F. occidentalis* over *T. urticae*, such that a preference was shown for thrips damaged leaves over mite damaged leaves in the absence of any prey. The time *Orius* would spend foraging was correlated with the degree of damage on the plant, leading the authors to propose a "giving-up rule".

Faeth (1992) manipulated herbivore levels of the leaf miner *Cameraria sp. nov.* (Davis) on *Quercus emoryi* to see if herbivore density affected the attraction of natural enemies. For a two year period, the trees were measured and there was no difference in percent of *Cameraria* killed by either predators or parasitoids for densities ranging from virtually 0% infestation to 75% of all leaves on a branch infested. Faeth concluded that this meant the plant gained no indirect defense from natural enemies in this system, regardless of whether more predators were initially attracted to the area.

Other Potential Systems

In a review by Dicke (1999), seven plant species were identified as producing quantitatively different head space volatiles for different inducing herbivores: apple, corn, cabbage, nasturtium, broad bean, tobacco, and cotton. In only two plants were qualitative differences (different components) found. In nine systems, predators were able to selectively respond to their favored herbivore over another herbivore given the same host plant;

however, in five systems there was no discrimination between hosts. Given research in herbivore foraging behavior (Janz and Nylin 1997), one would expect specialist foragers would devote greater resources towards information integration, such as host plant volatiles.

Several systems can demonstrate either the production of plant volatiles following herbivore induction, or predator/parasitoid response to host presence, but have yet to connect the two experimentally. Alfalfa (*Medicago sativa*) produces induced defenses against *Spodoptera littoralis*. Agrell et al. (2003) measured increased concentrations of saponin components in induced leaves, which is an insect growth inhibitor. While this does not necessarily indicate any tritrophic interactions, it does chart the induction over time, showing an increase in induced effects (a.k.a. decreased feeding) on day 5 and 7 after induction, but not on days 1, 9, or 14.

Spodoptera littoralis also showed feeding behavior changes with induced tomato (*Lycopersicon esculentum*) leaves. When offered a wounded plant, larvae took fewer meals and moved their feeding towards the base of the plant; when starved larvae would feed on wounded leaves, but took shorter meals (Barker et al. 1995). While this behavior does have direct effects on the plant's fitness, it may also have indirect effects if the change in larval behavior indicates increased preparedness for predator attacks.

A plant-plant volatile signaling mechanism was demonstrated for lima beans infested by *Tetranychus urticae*. Lima bean plants sharing air space with induced plants began producing green leaf volatiles from uninfested leaves (Arimura et al. 2001). An airborne signal was also found between wild tobacco and sage brush, where tobacco downwind of injured sage was less likely to receive injury and in caged experiments was less attractive than tobacco farther from the sage (Karban 2001). While interplant signaling can be a useful

direct defence against herbivores likely to migrate between plants, the utility of interplant signaling at a tritrophic level has not been adequately addressed. Additionally, an herbivore-induced airborne volatile signaling mechanism was demonstrated in *Alnus glutinosa*, the black alder tree (Tscharntke et al. 2001). This last example is especially interesting as the authors point out that given the size of many tree species, volatile signals may be an effective way to communicate within the tree canopy, and that plant-plant signaling is a side effect of using a within plant signaling mechanism.

Lygus hesperus has been shown to induce volatile productions in both cotton and corn (Rodriguez-Saona et al. 2002). Oddly enough, the volatiles produced in cotton were the same volatiles produced by *Spodoptera exigua* damage even though the two insects have very different feeding habits, indicating a lack of specificity in the system.

Bruchid beetles (*Callosobruchus chinensis*) were shown to induce cowpeas to produce the volatile tridecanone. Adult female beetles avoided cowpeas that had been infested by conspecifics (Babu et al. 2003). What makes this a unique situation is that the beetles infest stored products, so the cowpeas are being induced without going through a normal plant vascular system.

Induced volatiles are supposed to be useful in systems where a predator is able to reduce herbivore populations to a degree where plant fitness is improved. This was found to be the case for the seed weevil *Ceutorhynchus sp. nov.* and its host plant *Hormathophylla spinosa*. The weevils destroy almost a fifth of total fruits produced, but when predators are excluded this rose to 40% of the fruit being destroyed (Gomez and Zamora 1994). While this system would seem to benefit from plant induction, there have been no reported induced volatiles. There has however, been some indication that the parasitoids are spatially arranged

in accordance with herbivore distribution, and that handling time is what prevents parasitoids from operating in a density dependent fashion.

Summary

Looking across the systems described here, there are many patterns in the specificity of predator response. While there is evidence that induced indirect defense is more specific than other forms of plant defense (Dicke and Takabayashi 1991), the question still remains how much specificity is necessary for predators and parasitoids to gain useful information from plants. An important conclusion from this review is that predator response to plant volatiles is not as precise as would be predicted if it were ecologically optimal. This includes cases where the predator responds even though the inducing host is of the wrong age (Coleman et al. 1999, Gouinguene et al. 2003) or of the wrong species (Rodriguez-Saona et al. 2002, van Poecke et al. 2003). Part of this apparent confusion may be due to overlap of the chemical signals (Rodriguez-Saona et al. 2002, Shiojiri et al. 2002, Du et al. 1998); however, if the signal is not indicative of a potential host, why should the predator respond at all?

Another pattern that has not thoroughly been explored is the preference of specialist predators and parasitoids for certain host plants of their generalist prey. Parasitoids of *Helicoverpa punctigera* (Bjorksten and Hoffman 1998), *Heliothis virescens* (De Moraes and Lewis 1999), *Plutella xylostella* (Liu and Jiang 2003), and *Aphidius colemani* (Storeck et al. 2000) all showed a preference for volatiles from a particular host plant within the wide host range of their specific prey. Similarly, predatory mites exhibited preference for their prey species at both the plant species and plant cultivar level (Dicke and Takabayashi 1991).

While a difference in chemical profiles between plants could explain how parasitoids are able to distinguish plant species, it does not explain why the preference was made.

One explanation for parasitoid preferences of host plants is that some plants may be more synchronized with their herbivore host, and thus be a better indicator. In the cases where a time course of induction has been studied (Gouinguene et al. 2001, van Poecke et al. 2001, Dicke et al., 1999, Agrell et al. 2003 , Mattiacci et al. 2001), there was often a considerable lag period between the time herbivory began and the time parasitoids could detect a signal, ranging from 12 hours (Gouinguene et al. 2001) to 5 days (Agrell et al. 2003). However, most induction studies are done within a day of the onset of herbivory. Additionally, few studies have looked for a diminution of signal once herbivores were removed, either testing attractiveness when the herbivore is still on the plant (e.g. De Moraes et al. 1998, De Moraes and Lewis 1999, Gouinguene et al. 2001, Gouinguene et al. 2003, Neveu et al. 2002, van Poecke et al. 2001), or only a short time following the removal of herbivores (e.g. Baehrecke et al. 1990, Liu and Jiang 2003, Bertschy et al. 2001, but see: Turlings et al. 1992).

Even less is known about the spatial scale of induction (Baldwin et al. 2006). The arrestment of parasitoids and predators to short-range olfactory plant cues has been documented in many systems (e.g. Baehrecke et al. 1990, VanLaerhoven et al., 2000, Bjorksten and Hoffman 1998, Jang et al. 2000), but long-distance attraction is less well understood. While plant volatiles are often considered to be important at attracting predators in from a distance (Vinson 1991), there is no systematic study of the radius of this attraction. Many of the attraction studies were done in wind tunnels and olfactometers of a set distance and controlled air flow, which does not elucidate the distance at which attraction can operate

nor the potential gains in foraging time that can be made from greater attraction. Of the described studies, few were tested in field conditions (De Moraes et al. 1998, Liu and Jiang 2003), and these indicated that host plants showing strong effects when isolated in wind tunnel studies were less attractive in the field. Understanding how the spatial patterns of plant volatiles impact the distribution of parasitoids could provide insights on successful parasitoid systems. Models of aggregation show that the stability of parasitoid-host systems can depend on how much spatial variation there is in the number of parasitoids per host density (Gross and Ives 1999).

A few systems have shown plant-plant signaling capabilities (Dicke and Bruin 2001), eliciting cues from non damaged plants sharing airspace (Dicke et al. 1990, Arimura et al. 2001, Karban 2001) or soil space with injured plants (Guerrieri et al. 2002), which might increase the radius of signal production (Preston et al. 2001). The impact of this behavior on the foraging parasitoids is unknown. Some authors argue that this will amplify the signal (Guerrieri et al. 2002) while others argue that this is a mechanism for plants to "cry wolf" (Bottrell et al. 1998).

Currently, empirical researchers have an implicit model of the value of host-induced plant volatiles. Louise Vet (2001) summarized the current assumptions with the following statements. "Nonprofitable plants are neglected and the area to be searched is thus significantly reduced. Hence, travel time in the field will decrease and host encounter rates will increase. This increase in searching efficiency is especially beneficial to parasitoids that are time limited…." She adds, "If the production of volatiles by plants and the resulting attraction of parasitoids is not linearly correlated to the density of hosts on these plants, plants can play a crucial role in determining the heterogeneity of attack rates."

Indeed most of the research in this field has focused on individual behavioral responses, assuming that the population level responses will occur as predicted. However, there is no current standard for quantifying the profitability of a plant's signal, especially considering its environmental context (Dicke et al. 2003). Additionally, the ability of plant signals to increase searching efficiency at a spatial scale larger than the individual plants, has yet to be conclusively demonstrated for any predator or parasitoid. A modeling approach may help generate predictive hypotheses that can be tested at the field level to complement our current knowledge of the system at smaller spatial scales.

Models may also help address one of the large remaining questions in this field (Takagi 1999). Herbivore-induced plant volatiles are useful to foraging parasitoids because they allow parasitoids to bypass the reliability-detectability problem. However, compared to direct defense or predation, parasitism kills herbivores more slowly, thus costing the plant more resources. Why should the most specific form of defense be in the most inefficient manner (Dicke and Takabayashi 1991)? To answer this, we need to know the costs and benefits of producing volatiles for a population of signaling and non-signaling plants (Janssen et al. 2002), and this type of question can be best addressed in a modeling framework.

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CHAPTER II

THE RELEVANCE OF HERBIVORE-INDUCED PLANT VOLATILES TO FORAGING PARASITOIDS: A DETERMINISTIC MODEL

Abstract

Parasitoids respond to volatiles that plants produce when injured by herbivores. There is a considerable body of literature identifying the chemical pathways that make herbivore-induced volatile production possible, but 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. We developed a model to examine this issue using general parameters from two tritrophic systems. The model uses herbivore oviposition, development, and mortality rates, linked to a range of plant volatile induction rates and cessation rates 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 number of hosts parasitized when the parasitoid focuses solely on the volatile-producing plants to when it forages randomly amongst all plants. Under some conditions parasitoids attack four times more herbivores if they focus on volatile-producing plants. However, when we simulate plants that take several days to cease volatile production following pupation or death of the herbivore, parasitoids lose any advantage by following volatile-producing plants. Also, the utility of the volatile cues is greater when a smaller proportion of plants are occupied by herbivores, indicating that fields saturated with volatiles may be detrimental to parasitoid foraging success.

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. DeMoraes and Lewis, 1999; Kaiser and Carde, 1991; Fatuoros et al., 2005; Jang et al. 2000). Hypotheses about the evolution of this plant/parasitoid interaction range from suggesting that plants evolved

volatile production to call in the third trophic level (Janssen, 2002; Turlings et al., 1992) to the simpler interpretation that plants passively produce volatiles that parasitoids happen to intercept (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 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 (Cortesero et al., 1997; Rose et al., 1998; van Poecke et al., 2003). Another potential source of misleading signals occurs when parasitoids respond to plants when the inducing herbivore is either too old to be attacked (Mattiacci and Dicke, 1995) or has left the plant (Mattiacci et al., 2001). Considerably less work has been done on these temporally misleading signals, and therefore an aim of this paper is to examine whether the timing of volatile emission is predicted to have an impact on the utility of signals.

In addition to natural sources of temporally misleading signals, crop breeding for stronger signals may produce situations where parasitoids have little incentive to respond. 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, Turlings and Ton 2006). One argument for this is that initial investigations show the metabolic costs to the plant may not be significant enough to rule out a constitutive volatile production (Turlings and Ton 2006). Several papers proposing 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, Turlings and Ton 2006); however, none of these papers specify how precisely plants need to be synchronized. For something that seems so obvious, there is a surprising lack of information on the plant timing, and while papers examine the chemical pathways plants use to produce volatile signals (e.g. De Vos et al. 2005), none have

suggested looking for genes that turn on or off at the cessation of herbivory as a logical next step.

As demonstrated by Holling (1959), predators' and parasitoids' foraging success is limited by their handling time, total available foraging time, and host encounter rate, which can be influenced by available host density and area of discovery. Predators and parasitoids can take advantage of many visual, olfactory, or auditory cues in their environment to optimize their host encounter rate. If herbivore-induced volatiles from plants can be used by the parasitoid to optimize any of these parameters, then response to the volatiles can increase parasitoid fitness. On the other hand, if parasitoid response to the volatiles increases handling time, decreases the available foraging time, or decreases the host encounter rate, the response to induced cues coming from the plant should be secondary relative to other cues.

The number of systems in which parasitoids use volatile signals indicates that there must be some advantage to using herbivore-induced plant volatiles; however, there are currently no studies that quantify this advantage. 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). Rosenheim's (1999) model on costs of oviposition, for example, drew many biologists' attention to the role of egg limitation on parasitoid fitness. Here we develop a model that complements Rosenheim's work on parasitoid fitness, as that model focuses on the costs incurred once a host has been identified while our model looks at possible costs incurred in the process of identifying a host.

In this paper, we describe a model that examines to what extent both the herbivore's life history and the temporal pattern of the plant's response to herbivory determine whether herbivore-induced volatiles can be useful cues in parasitoid host finding. Parameters for the model are taken from two specific tritrophic systems that would be considered candidates for genetic modification of volatile signal production. The first system we considered 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 wasps if moths do limit their oviposition. The second system we considered consists of *Brassica oleraceae*, *Pieris rapae*, and *Cotesia glomerata*. The parasitoid, *C. glomerata* can attack all instars of *P. rapae*, however parasitoid larvae suffer greater mortality due to increased encapsulation if laid in third or later instar caterpillars (Mattiacci and Dicke 1995). For this system, we looked at the consequences of narrowing the window of available host instars that a parasitoid could attack.

Overall, we expected that signals more closely synchronized with host presence would be more relevant to foraging parasitoids, so that a field of plants that could respond to herbivory in one day would produce more relevant signals than a field of plants that took five days to respond to herbivory. However, before constructing this model, we did not know whether the cost of delaying a signal from one day to five days would be crippling 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 effect or a minor effect. Our use 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.

Methods

Incorporating plant volatiles into the Holling's equation- The fitness of a solitary parasitoid can be directly correlated with the number of hosts successfully attacked, as each host can lead to one offspring (Lawton et al. 1975). 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.

$$Rel = \frac{N_{Asig}}{N_{ARan}} \qquad \text{(Eq.1)}$$

Where ***Rel*** is the signal relevance to the parasitoid, $\mathbf{N_{ASig}}$ is the number of hosts attacked by parasitoids that focus only on plants that are producing herbivore-induced volatile signals, and $\mathbf{N_{ARan}}$ 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.

$$N_A = \frac{T_t * a * x}{1 + a * b * x} \qquad \text{(Eq. 2)}$$

Where $\mathbf{T_t}$ 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:

$$Rel = \left(\frac{T_{sig} * a_{sig} * x_{sig}}{1 + a_{sig} * b_{sig} * x_{sig}} \right) \Bigg/ \left(\frac{T_{Ran} * a_{Ran} * x_{Ran}}{1 + a_{Ran} * b_{Ran} * x_{Ran}} \right) \qquad \text{(Eq. 3)}$$

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; Neveu et al., 2001; Rodriguez-Soana et al., 2001), and that it is contained to a single plant. The density of hosts, x, in the Holling model is traditionally provided in hosts/m^2, but because induction is occurring at the level of plants, not meters, we assume 1 plant/m^2, and thus give our density measurements in "hosts/plant".

The total time available $\mathbf{T_t}$ is the amount of time the parasitoid remains foraging in the relevant environment. We assume that $\mathbf{T_t}$ 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. In order to keep all time units equal, $\mathbf{T_t}$ 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 must 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 m/s) and multiply by the density of plants (plants/m). Multiplying $\mathbf{T_t * a}$ 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.

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 that the parasitoid could encounter. The more hosts encountered, the more time must be invested in 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 leaves the plant. The total time spent in handling hosts is **a * b * x**. The actual number of plants a parasitoid can visit is then **a * x *** the time available for searching, which is only a fraction of the total time available for foraging. This fraction can be calculated as: $\mathbf{T_t / (1 + a* b * x)}$.

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). We will explore the impact of two mechanisms- increasing giving-up time in the presence of signaling plants and bypassing non-signaling plants.

1) Increasing giving-up time. When encountering herbivore- induced plant volatile cues, some parasitoids search plants longer before leaving (Nealis, 1990; Kester and Barbosa,

1991; 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 study the impact of giving-up time, we must alter the Holling equation (Eq. 2) to include a term for giving up time.

$$N_A = (T_t * a * x) / (1 + a * b * x + a * c * E + a * c/2 * O) \qquad \text{(Eq. 4)}$$

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 * c * E**, which is the probability of a parasitoid landing on an empty plant (**a * 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 * c /2 * O**.

There are two ways that volatile signals can impact the parameters in Eq. 4. The first is that the value for **c** may be different for parasitoids following signals compared to randomly foraging; indeed, we would expect $\mathbf{c_{sig}} > \mathbf{c_{ran}}$, if following signals increases the amount of time that a parasitoid will spend on a plant without finding a host. Additionally, the values for **E** and **O** depend on the density of plants, and if parasitoids following signals perceive plant densities differently, then this can also change the number of hosts attacked.

2) Bypassing non-signaling plants. 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 the parasitoid maintains the same flight speed and handling time, but restricts its environment to only signaling plants. The parasitoid may therefore encounter a different density of hosts if it preferentially forages in signaling plants rather than randomly foraging. The impact this has on the signal relevance depends on the underlying host density and 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 an herbivore or empty (E); 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:

$$x_{Sig} = n_{SO} / (n_{SO} + n_{SE}) \quad \text{(Eq. 5a)}$$

$$x_{Ran} = (n_{SO} + n_{NO}) / (n_{SO} + n_{NO} + n_{SE} + n_{NE}) \quad \text{(Eq. 5b)}$$

All other variables being held constant, if ($\mathbf{x_{Sig} > x_{Ran}}$), signal relevance will be greater than one, and if ($\mathbf{x_{Sig} < x_{Ran}}$), 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:

$$E_{sig} = n_{SE} / (n_{SO} + n_{SE}) \quad \text{(Eq. 6a)}$$

$$E_{Ran} = (n_{SE} + n_{NE}) / (n_{SO} + n_{NO} + n_{SE} + n_{NE}) \quad \text{(Eq. 6b)}$$

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:

$$N_{Asig} = \frac{T_t * a_{sig} * \left(\frac{n_{SO}}{n_{SO} + n_{SE}}\right)}{1 + a_{sig} * b_{sig} * \left(\frac{n_{SO}}{n_{SO} + n_{SE}}\right) + a_{sig} * c_{sig} * \left(\frac{n_{SE}}{n_{SO} + n_{SE}}\right) + a_{sig} * \frac{c_{sig}}{2} * \left(\frac{n_{SO}}{n_{SO} + n_{SE}}\right)} \quad \text{(Eq. 7)}$$

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

(Eq. 8)

Finally, when parasitoids bypass non-signaling plants, 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 therefore be adjusted to account for the increase in distance:

$$a_{sig} = a_{Ran} * \sqrt{\frac{n_{SO} + n_{SE}}{n_{SO} + n_{SE} + n_{NO} + n_{NE}}}$$

(Eq. 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 the plants transitions 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 larva 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. Because the herbivore mortality rate depends on larval age, the model includes different infestation age classes for each day of the 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. 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 the plant is simultaneously occupied by a younger larva.

When a plant is re-infested, 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 of volatiles 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 timestep. The induction rate at which plants move from N to S after the onset of herbivory is set at values ranging from one to five days for this model. The relaxation rate at which plants move from S to N following the cessation of herbivory is also fixed at values ranging from one to five days.

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 density on signal relevance, we hold **a**, **b**, and $\mathbf{T_t}$ constant, using parameters from the literature for the two system examples we provide. Table 1 summarizes the assumptions made in the construction of this model.

Model Parameters. We used life history data on *Heliothis virescens* and *Pieris rapae* (Robbins and Henson 1986) for setting parameter values in the model. *Heliothis virescens* is a generalist in the family 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. *Cardiochiles 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 cotton, regardless of the most dominant host plant available (DeMoraes and Lewis, 1999, Tillman and Mullinix 2003). While difference in volatile production may explain how the 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 the different host plant preferences.

Daily mortality rates for *Heliothis virescens* were calculated for each larval stage using data from Johnson and Gould (1992). Because *Heliothis virescens* varies widely in its survival rates, a low mortality and a high mortality scenario are examined (see Table 3). *H. virescens* adults have been shown to 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 2. 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 $\mathbf{T_t}$ of 3 hours or 10,800 seconds. On the host plant tobacco, parasitoids spend 11.6 seconds hovering and 11.7 seconds searching around a plant for a total of 23.3 seconds searching per plant, giving an estimate of 0.043 plants per second for **a**. The handling time for oviposition and preening (**b**) was 20.5 seconds 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 seconds for wasps on tobacco. *C. nigriceps* exhibits a marked preference for hosts on tobacco in the field, and the time spent on agony search was nearly twice as long on tobacco as on cotton. Therefore, we tested the sensitivity of c by setting $\mathbf{c_{sig}}$ and $\mathbf{c_{Ran}}$ both at 128.7 seconds, the actual estimate for **c**, and at 64.4 seconds, half the estimate for **c**.

The *Pieris 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 Pieridae family that specializes on plants in the Cruciferae family, including crops such as cabbage, broccoli, and Brussels sprouts, and the experimental model system, *Arabidopsis thaliana* (Courtney, 1986). A major parasitoid for *P. rapae*, *Cotesia glomerata*, is restricted to ovipositing in only the first two instars of *P. rapae*, but can not 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 three days of feeding by *P. rapae*. Additionally, a wind tunnel study found that Brussels sprouts fed on by *Pieris brassicae,* a close relative to *P. rapae,* were most attractive to *C. glomerata* three days after feeding and ceased being attractive to the parasitoids one day after the herbivores were removed (Mattiacci et al., 2001).

P. rapae larvae go through five larval instars of approximately three days each. Daily mortality rates were taken from Dempster (1967) (see Table 3). Because *C. glomerata* specializes on the first two instars of *P. rapae*, encountering a plant with a fifth instar larva would have the same effect as encountering an empty plant. 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 successfully attack. We examined the impact attack preference has on signal relevance by setting the attack preference at 3 days (first instar), 6 days (second instar), 9 days (third instar), 12 days (fourth instar), and 15 days (fifth instar).

In order to calculate signal relevance for this system, we can use parameter estimates derived from the literature (see Table 2). The parasitoids are most active in the late morning and early afternoon hours (Kaiser and Carde 1991), so we assumed a maximum of four hours of foraging per day, the total time ($\mathbf{T_t}$) is 14,400 seconds. 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 seconds, and the handling time (**b**) was 13.1 ± 3.9 seconds. 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/second.

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 rapae* system, while area of discovery and total foraging time were shorter for the *Heliothis* system. This would lead us to predict that for one foraging day *Cotesia marginiventris* would be capable of attacking more *Pieris rapae* than *Cardiochiles nigriceps* is capable of attacking *Heliothis 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 low occupation rates(Figure 2). 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. The first and simplest hypothesis that we tested is that changing the occupation rate, which is the fraction of plants newly occupied at each time step, would result in a change in the percent of plants infested with larvae. Figure 3 shows how percent

infestation in the field changes with the occupation rate for both high and low mortality scenarios, and for both limited and multiple oviposition scenarios in a simulated field occupied by *Heliothis virescens*. 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. In the multiple oviposition scenario, each stage class is multiplied 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. In the limited oviposition scenario, the asymptote is less than 1.0 due to the ovipositing host's avoidance of plants induced and empty (SE). As described in the Methods section, the fact that the multiple oviposition scenarios also reach an asymptote below 1.0 is a result of the model only following the youngest larva on a plant. 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 (Figure 4a). The N_A for random foraging increases following 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 responding 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 (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 (Figure

4b). 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 will present results for occupation rates less than 0.5, as data for higher occupation rates both represents unrealistic field densities and is less reliable due to the inherent bias in the model towards 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 days had little to no effect on the relevance of the signal (Figure 5a). 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 rate, 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 five day induction delay leads to a lower *Rel* than a one day induction delay, 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 are 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 (Figure 5c).

Relaxation Delay. In most cases, as the delay for plant signal relaxation increased from 1 to 5 days, the relevance of the signal decreased (Figure 5b); the only exception was

the case when host stage attack is limited to first instars (Figure 5d). 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 *Heliothis 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 (Figures 6a and b); 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_{sig} will not be affected by the transition but x_{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, reducing the n_{SO}, which has the effect of decreasing a_{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 *Heliothis virescens* life table, the number of transitions from NO to NE are 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 great enough so that the area of discovery is similar for both foraging strategies, the impact 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.

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 (Figures 6a and b). By avoiding signaling plants, the 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 this behavior has 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.

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 only attack first instar *Pieris rapae* would have a $Rel > 1$ if the host plant induced after one or two days, but $Rel < 1$ if host plant induction took longer than three days (Figure 5c). In the case of higher induction delays and a parasitoid limited to first instars, the SO state only occurred 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.

Giving-up time. We compared the effects of halving the giving-up time, **c**, in the *Heliothis* system because the giving-up time (**c**) is nearly twice as high for *C. nigriceps* on tobacco as on cotton, and therefore we see the natural variability for that parameter is in this system. If we assume that the value c_{sig} in Eq 7 is equal to c_{ran} in Eq 8, then *Rel* is greater for the longer giving-up time, but not to such a degree that the parasitoid should change foraging strategy (Figure 7, comparing c/c to half/half). If we assume that arrestment operates by increasing the giving up time when following signals but not when randomly foraging, we can set $c_{ran} = c_{sig} / 2$. This response reduces *Rel*, and for a wide range of occupation rates, *Rel* is less than one (Figure 7, c/half). On the other hand, if we set $c_{sig} = c_{ran}/ 2$, this increases the signal relevance to well above 1 for all occupation rates (Figure 7, half/c). It is important to note that we assume that if a plant is occupied by a host, the parasitoid will find it no matter how short the giving up time so this may introduce a bias to our results.

Discussion

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

Additionally, we were able to look 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.

The *Heliothis* system brings up a conundrum when it comes to parasitoid foraging. *C. nigriceps* clearly prefer tobacco over cotton when foraging, but the additional giving-up time in tobacco appears to be disadvantageous according to this model. A possible explanation for this is that in nature the probability of finding a host increases the longer a parasitoid remains on a plant, such that increasing the giving-up time also increases the probability of finding a host. However, the fitness gains for *C. nigriceps* by investing extra foraging time on

tobacco versus cotton have not been investigated in our model that assumes that all hosts are found without regard to giving up time.

Implications for Pieris System. Because *C. glomerata* has a narrow range of host stages it attacks, 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 *Pieris 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 two days 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 third instar because *C. glomerata* specifically forages on the first two instars. However, in systems where it has been measured, the plants responded to herbivory with volatile production well before the third instar would have been reached (Mattiacci et al. 2001; De Vos et al. 2005; Geervliet et al. 1998).

General Conclusions. Results from this model identify several biological parameters that should be more thoroughly studied empirically. The relationship between herbivore density, plant signal 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 important point is that a delay in the initiation or cessation of signal production may, in certain conditions, decrease signal relevance for a foraging parasitoid. It is not enough to simply measure whether volatiles are produced and whether parasitoids can physically respond 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). Natural variation in plant signaling synchrony may be present. There are many agriculturally important systems in which parasitoids of generalist crop pests respond more strongly to

some host plants than others (e.g. Oppenheim and Gould, 2002; DeMoraes et al., 1998; Fritzsche Hoballah et al., 2002; Liu and Jiang, 2003). Additionally, in a few studies it has been found that parasitoids can respond more strongly to some lines within a plant species, indicating that genes for the volatile cues may have inadvertently been bred out of some cultivars (Fritzsche Hoballah et al. 2002, Lou et al. 2006). Part of this discrimination may be due to the specific chemicals comprising the plants' volatile cues, but simply a difference in blends does not explain why a parasitoid would choose to follow one blend over another. These preferences may be due to certain plant-host complexes producing more relevant signals than other plant-host complexes.

In addition to looking at the presence or absence of 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. 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 the threat of herbivory is removed. Within the scenarios examined using our model, we found that the greatest increase in parasitoid attack rate due to presence of signals was four fold. Plant breeders must determine if an increase of four fold or less will lead to economic and environmental gains substantial enough to justify a complex breeding program.

Lastly, the value gained by a parasitoid's response to plant volatiles is partly attributable to herbivore behavior. In cases where *Heliothis virescens* were allowed to oviposit on plants regardless of their signaling or infestation status, the parasitoid's foraging success was never decreased by following plant volatile signals. However, when herbivores avoided ovipositing on plants that were either occupied or were still producing volatiles, there was a range of plant response parameters in which the parasitoid could be at a disadvantage if it followed the volatiles. This was especially true when herbivore mortality was high.

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; Fukishima et al., 2002; Kester and Barbosa, 1991) to follow plant produced volatile cues. A parasitoid that can learn, may adjust its foraging strategy between

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 time scale.

There are many possible mechanisms through which herbivore-induced plant volatiles may act on the variables in this model. We chose to focus on bypassing non-signaling plants and increasing giving-up time, but there are other processes that may be at work. By examining the assumptions we made, we 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 slow down its flying rate and increase its turning radius, then this impacts the number of plants the parasitoid can land on over time ($\mathbf{a_{Sig} \leq a_{Ran}}$).

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, $\mathbf{T_{tSig} \leq T_{tRan}}$ 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

following a successful oviposition, then this can lead to a difference in handling time for signaling and random plants ($\mathbf{b_{Sig} > b_{Ran}}$).

We assumed that the probability of finding a host if a plant was infested was 1.0. In truth, finding a host, even when the correct environment is identified, is not guaranteed. By searching longer in patches that produce herbivore-induced volatiles, the parasitoid increases the likelihood of encountering its host (Kareiva and Odell 1987). To improve the model, a term for the probability of finding a host as a function of time, would need to be coupled with the term for giving-up time, **c**.

Because plants were categorized by their youngest infesting larvae, cases where the youngest larva dies first were misclassified. This biases the model towards empty plants in the multiple occupation scenarios because there is higher mortality for first instar larvae, especially in the case of *Heliothis virescens*. This bias is especially troublesome at the higher occupation rates where multiple occupation is more likely to occur. We plan to further address this shortcoming in a spatially explicit model that will allow us to follow the fate of multiple larvae on a single plant.

The value of this 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. For example, given a parasitoid that selectively forages on the youngest instars of its host, we can predict that it should follow plant volatiles only if plants can induce before the first herbivore molt. Likewise, we can predict that if herbivores actively avoid ovipositing on occupied plants, parasitoids should be more likely to respond to volatiles from plants that are able to quickly relax signal production. Additionally, this model is general enough to be used for analysis of parasitoid/predator response to other types of cues. Using the same classification of Signaling, Non-signaling, Occupied, and Empty plants, the relative importance of visual cues of herbivory for foraging predators could also be examined. By formulating a definition of signal relevance, there is now a way to analyze the costs and benefits for a parasitoid following herbivore induced plant volatiles, or any other environmental cue.

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Table 1. Assumptions of the model.

•Induction is systemic and limited to a plant's own airspace (no plant – plant) signaling. •Plants are spaced at 1 plant per meter. •The field is large enough for parasitoids not to exhaust host resources before foraging time expires. •There is no previous parasitism or competition through superparasitism. •Parasitoids will fly in a straight path to the nearest neighbor from their current location, and in the case of signaling, they will fly to the nearest signaling neighbor. •T_t and b remain constant for parasitoids regardless of whether they follow signals or forage randomly. •The probability of finding a host if the plant is occupied, is equal to 1. •When a plant is reinfested by herbivores, the youngest larva is the only one that survives the encounter.

Table 2. Variables in the model

Parameter	*Heliothis virescens* *Cardiochiles nigriceps*	*Pieris rapae* *Cotesia glomerata*
Tt (sec)	10,800	14,400
a (plant/sec)	0.043	0.33
b (sec/hosts)	20.5	13.1
c (sec/plant)	128.7	73.5
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[1]	Limited and Multiple	Multiple
Host Attack Stage (instar)	5	1 - 5

[1] '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).

TABLE 3. DAILY MORTALITY RATES

		Heliothis virescens		*Pieris rapae*	
Day	Instar	Low Mortality	High Mortality	Instar	Mortality
1	1	0.12	0.33	1	0.1872
2	1	0.12	0.33	1	0.1872
3	1	0.12	0.33	1	0.1872
4	1	0.12	0.33	2	0.0874
5	2	0.03	0.26	2	0.0874
6	2	0.03	0.26	2	0.0874
7	2	0.03	0.26	3	0.0842
8	3	0.03	0.21	3	0.0842
9	3	0.03	0.21	3	0.0842
10	3	0.03	0.21	4	0.1373
11	4	0	0.03	4	0.1373
12	4	0	0.03	4	0.1373
13	4	0	0.03	5	0.2331
14	5	0	0	5	0.2331
15	5	0	0	5	0.2331
16	5	0	0	0	0
cumulative:		0.51	0.96		0.91

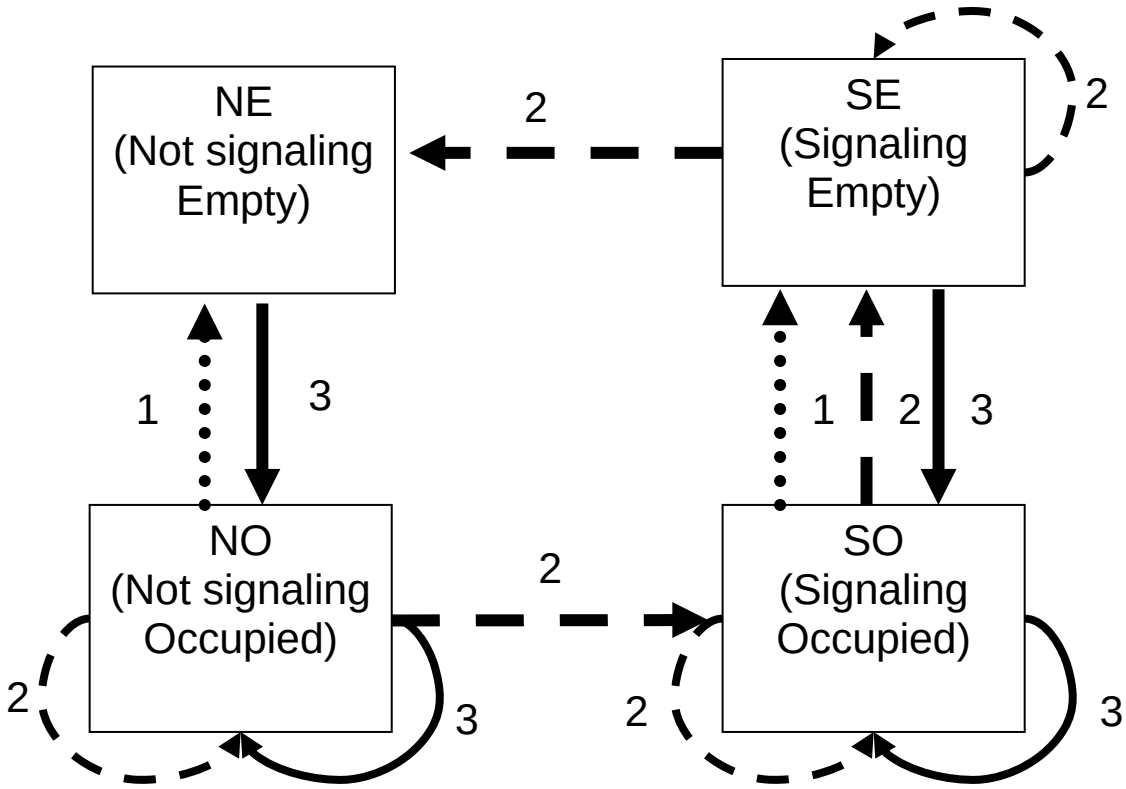


Figure 1. Flow diagram describing transitions between the four plant states, with each plant state represented by a box. Age classes of herbivores are modeled within each of the occupied (O) states, and relaxation rate-time classes are modeled within the signaling empty (SE) state (not shown). Each time 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.

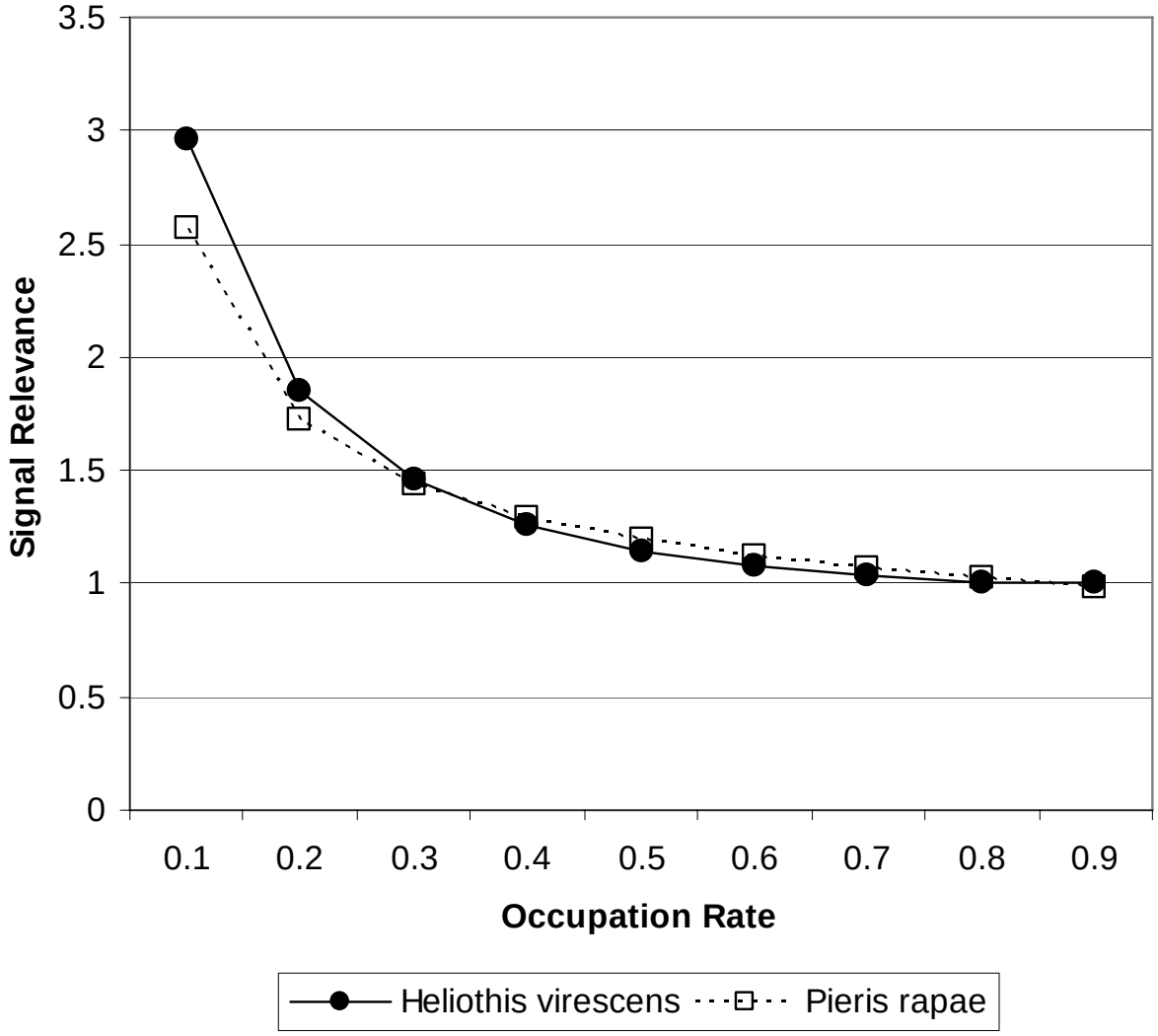


Figure 2. A comparison of the *Heliothis virescens* and *Pieris rapae* systems. For both systems, plant induction and relaxation delays were set at 1 day, multiple occupation was allowed, the parasitoid attack preference was for all five instars, and mortality was set at high. Occupation rate was varied from 0.1 to 0.9. All other parameters come from the values in Table 2.

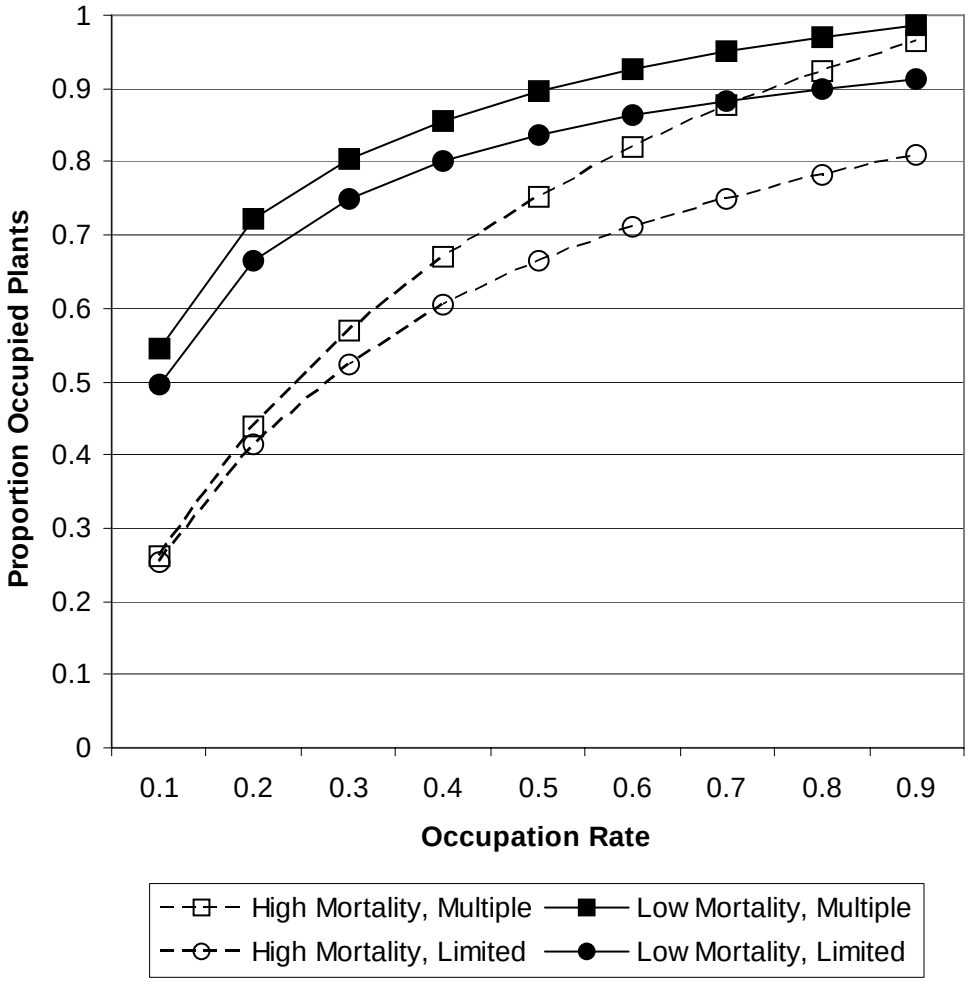
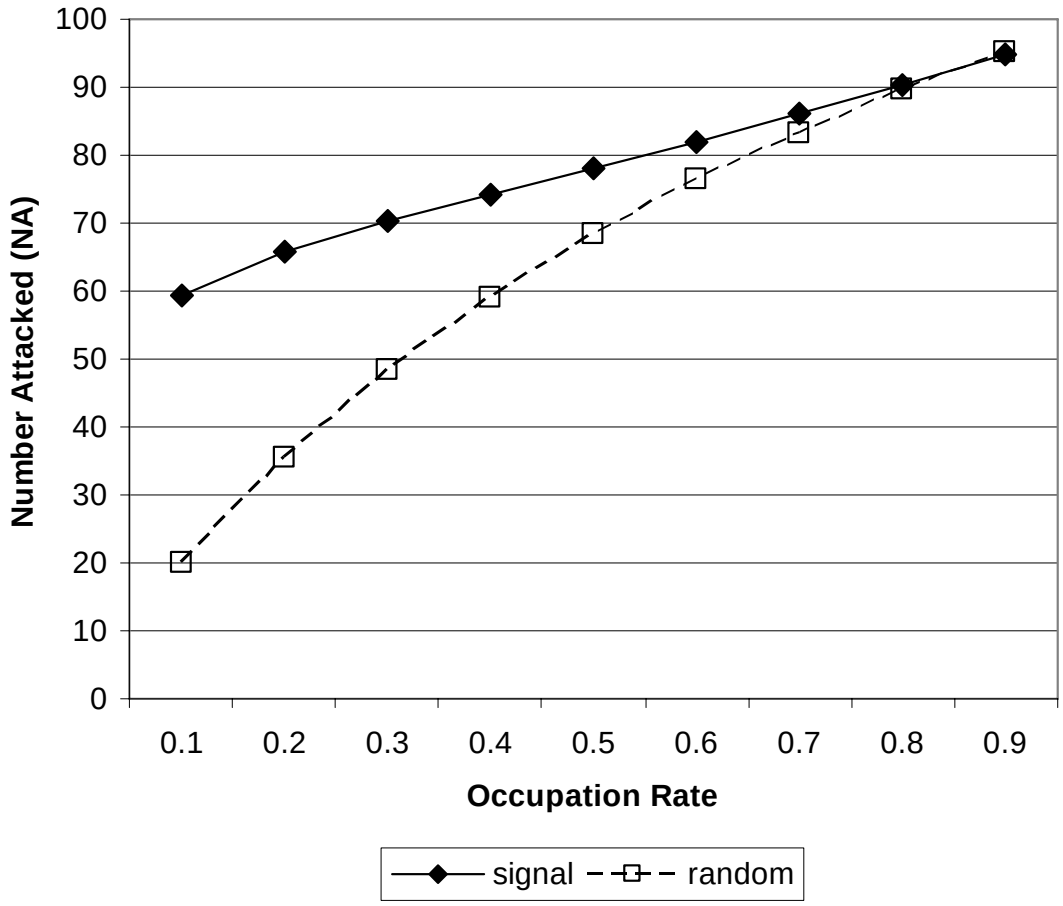


Figure 3. The relationship between Occupation Rate and proportion of plants occupied. The above results are for *Heliothis virescens* with one day induction delay and one day relaxation delay. High and Low Mortality rates are found on Table 2. "Limited" means new larvae only infest not signaling, empty plants. "Multiple" means new larvae can infest any plant including those already infested.

Figure 4. The Impact of Occupation Rate. These sample data came from the parameters of high mortality and multiple oviposition for *Heliothis 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).

4a:


100
90
80
70
60
50
40
30
20
10
0
Number Attacked (NA)
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
Occupation Rate
signal
random

4b:

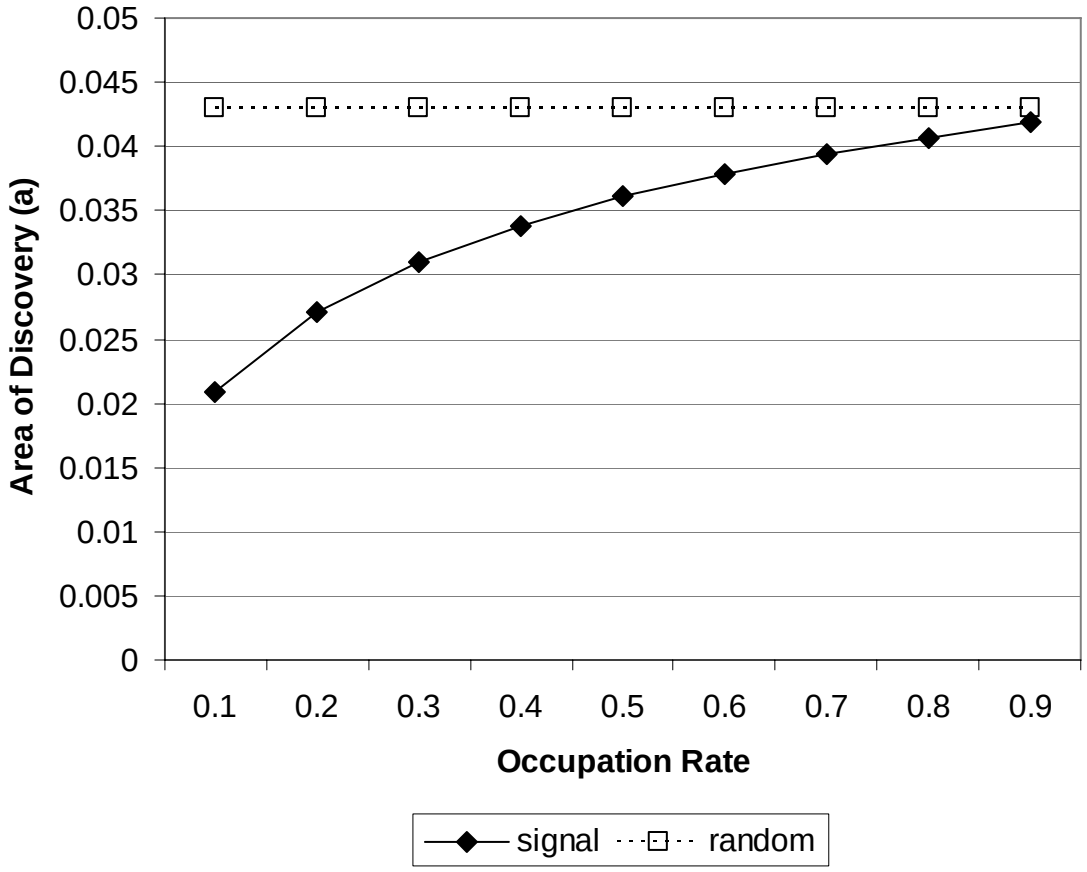
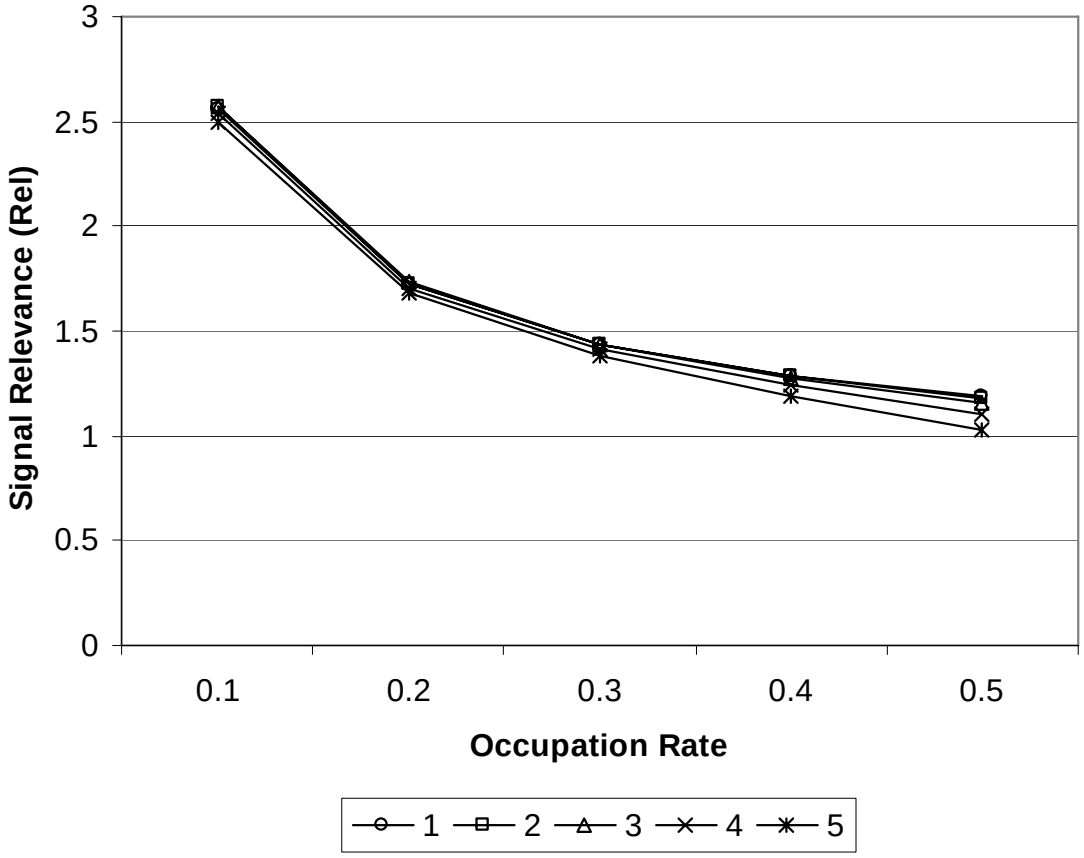
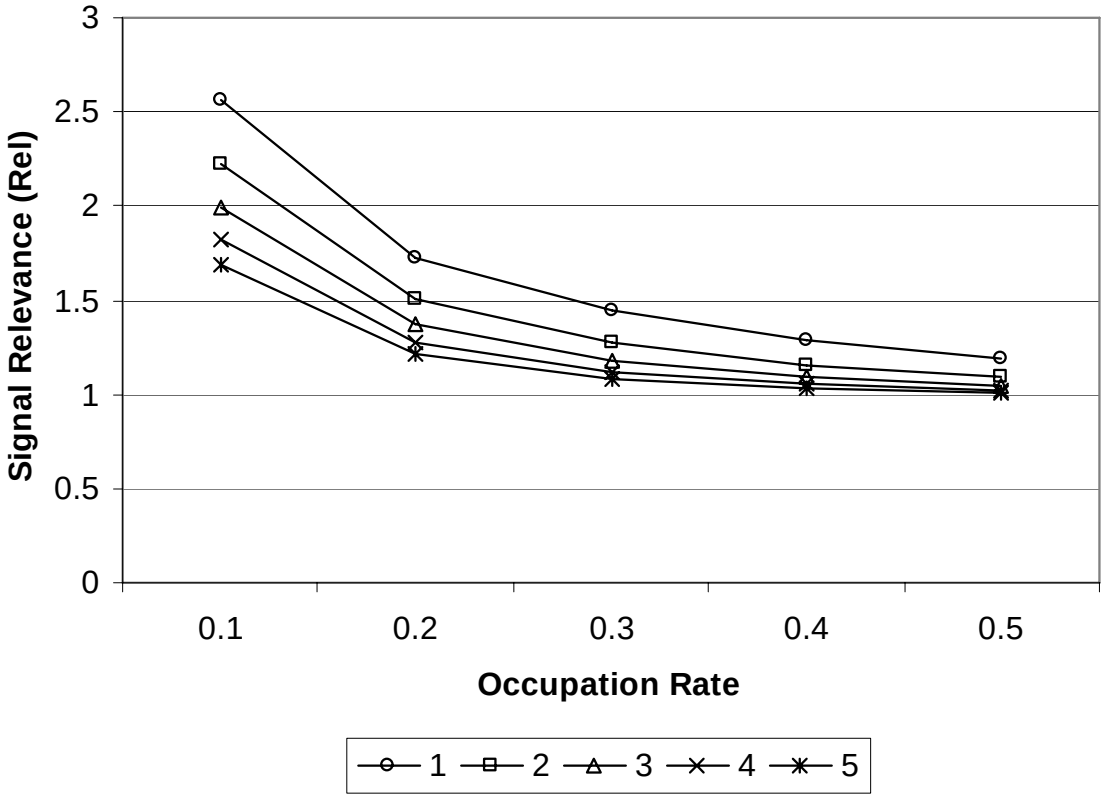

0.05
0.045
0.04
0.035
0.03
0.025
0.02
0.015
0.01
0.005
0
Area of Discovery (a)
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
Occupation Rate
signal
random

Figure 5. 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 for *Pieris rapae* and *Cotesia glomerata*. a) Numbers in the legend reflect days for induction delay. Relaxation delay was fixed at 1 day. 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 day, and host stage attack preference was fixed at fifth instar. c) Numbers in the legend reflect days for induction delay. Relaxation delay was fixed at 1 day. 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 days, and host stage attack preference was fixed at first instar.

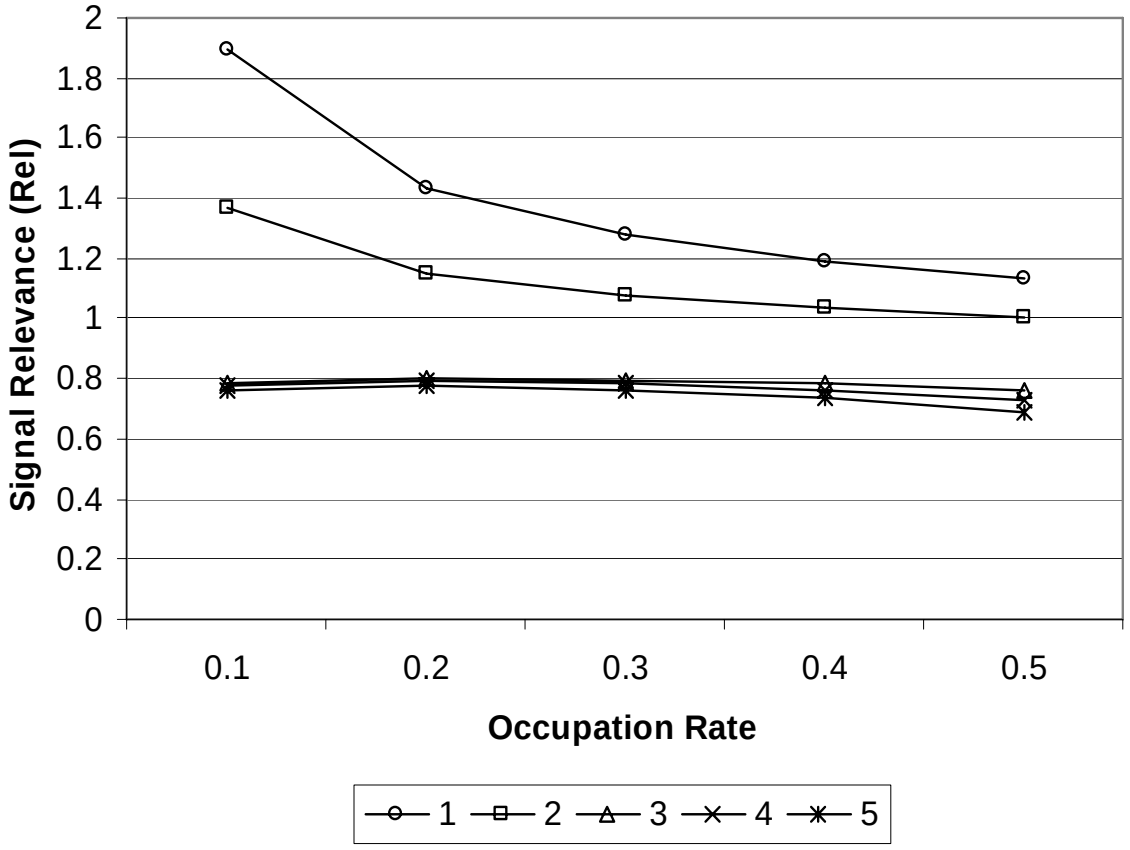
5a:


3
2.5
2
1.5
1
0.5
0
Signal Relevance (Rel)
0.1
0.2
0.3
0.4
0.5
Occupation Rate
1
2
3
4
5

5b:


3
2.5
2
1.5
1
0.5
0
Signal Relevance (Rel)
0.1
0.2
0.3
0.4
0.5
Occupation Rate
1
2
3
4
5

5c:


Signal Relevance (Rel)
2
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
0.1
0.2
0.3
0.4
0.5
Occupation Rate
1
2
3
4
5

5d:

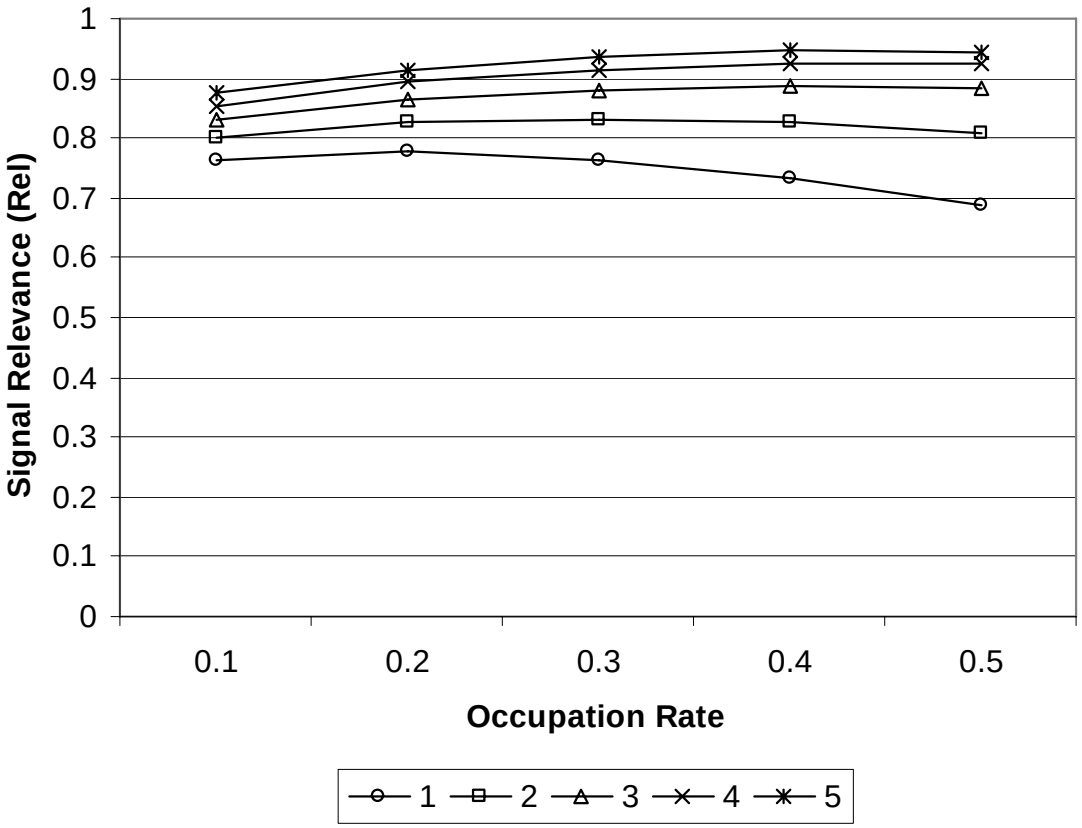
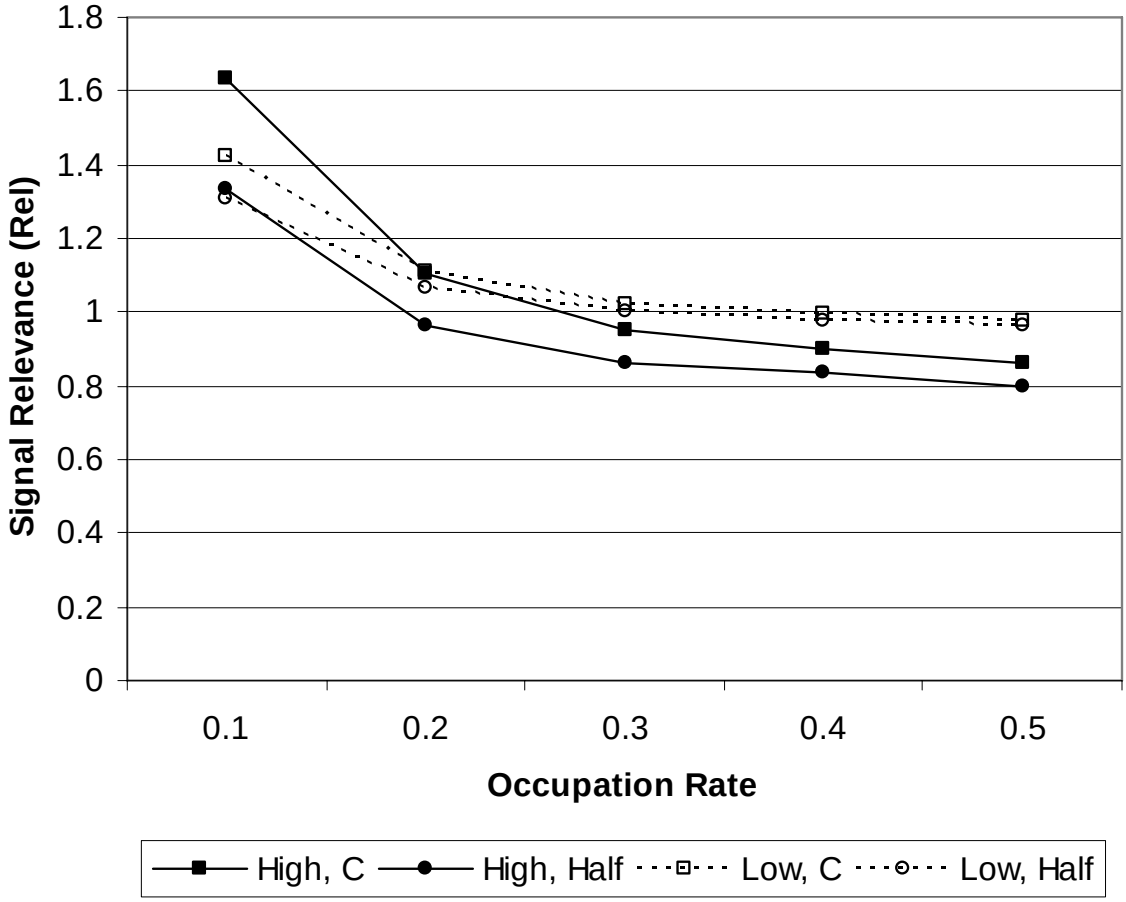
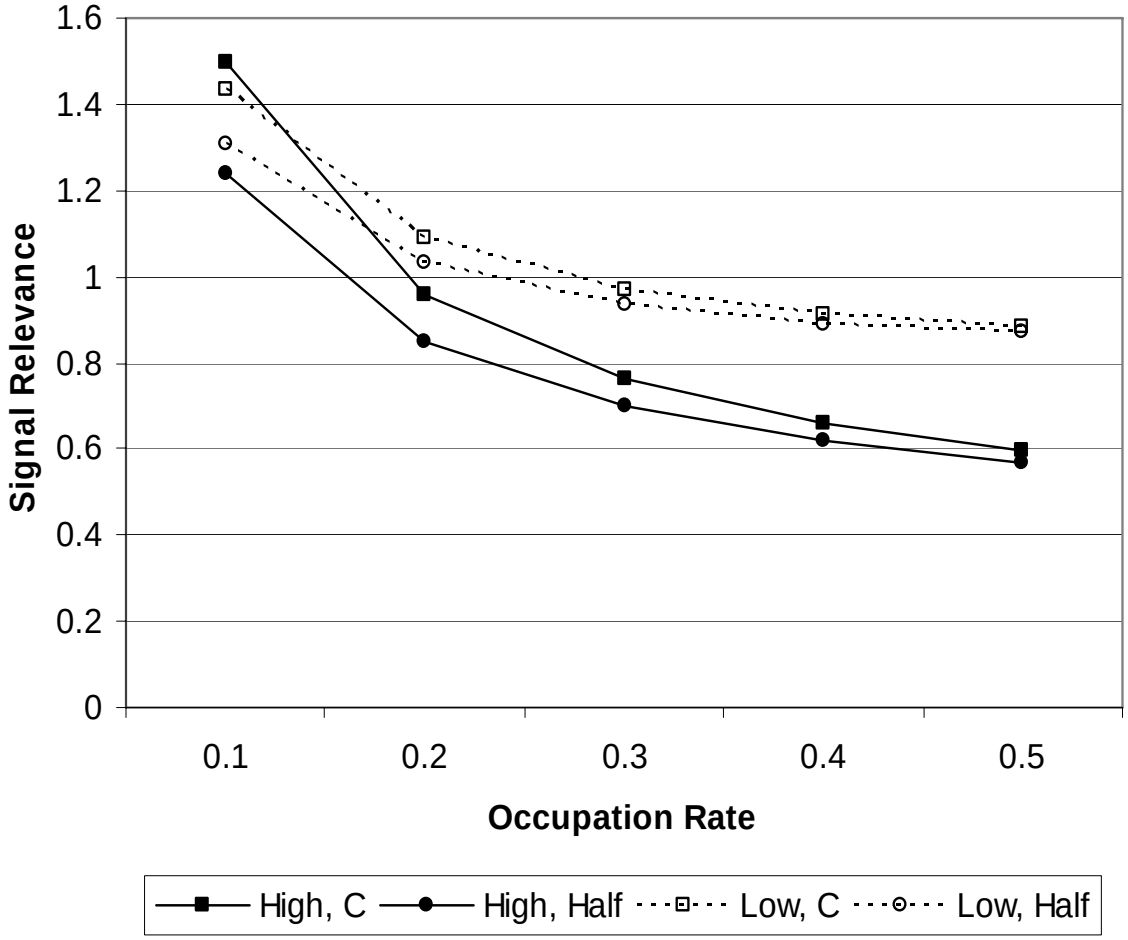

Signal Relevance (Rel)
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0.1
0.2
0.3
0.4
0.5
Occupation Rate
1
2
3
4
5

Figure 6. The relationship between Mortality Rate, Parasitoid Foraging Parameters, Host Oviposition and Signal Relevance. Parameters were set for *Heliothis virescens*; plant induction and relaxation delays were both set at 5 days. In the legend, "High" and "Low" refer to the high and low mortality values on Table 3. "C" refers to the value for **c** on Table 2, 128.7 seconds, and "Half" refers to half that value, 64.4 seconds. a) "Multiple" oviposition was used, which means an infested plant could be reinfested. b) "Limited" oviposition was used, which means only nonsignaling, empty (NE) plants could be infested.

6a:


1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
Signal Relevance (Rel)
0.1
0.2
0.3
0.4
0.5
Occupation Rate
High, C
High, Half
Low, C
Low, Half

6b:


1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
Signal Relevance
0.1
0.2
0.3
0.4
0.5
Occupation Rate
High, C
High, Half
Low, C
Low, Half

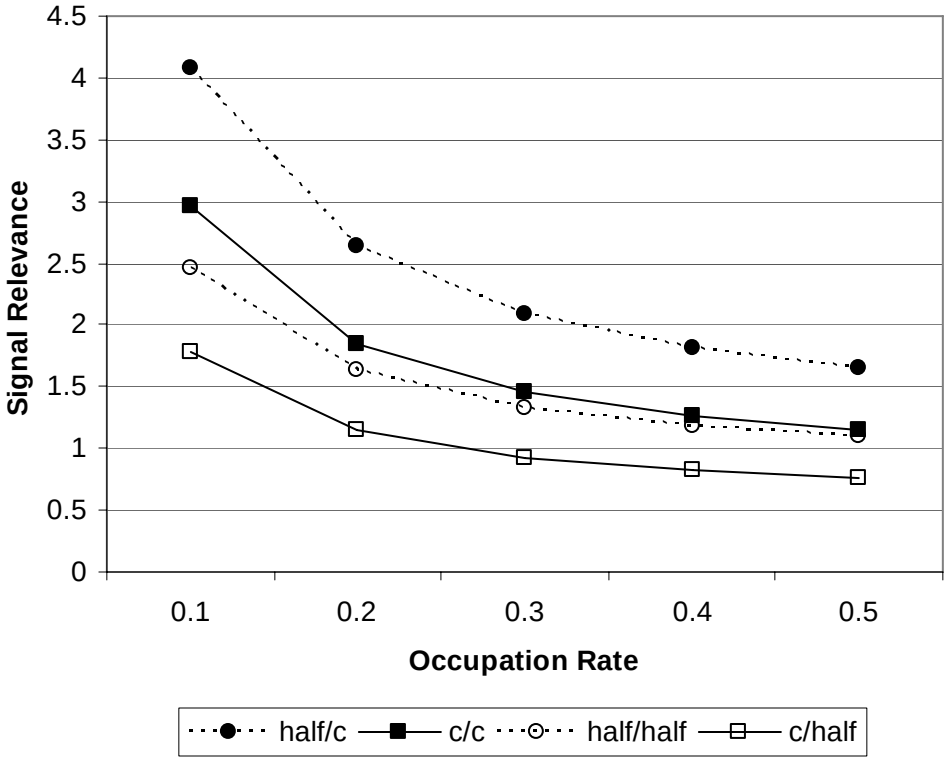


Figure 7. The Impact of Arrestment on Signal Relevance. For the graph below, *Heliothis virescens* mortality rate was set at "high", oviposition was set at "multiple", and plant induction and relaxation delays were both set at 1 day. In the legend, "c" refers to the estimated giving-up time of 128.7 seconds and "half" refers to half that value, 64.4 seconds; the first word refers to the parameters used in Eq. 7, and the second word refers to the parameters used in Eq. 8. So, for example, "half/c", means that csig was 64.4, and cran was 128.7 for that simulation.

CHAPTER III

Impact of Herbivore-induced Plant Volatiles on Parasitoid Foraging: A Spatial Simulation Analysis for *Cotesia rubecula, Pieris rapae,* and *Brassica oleracae*

Introduction

Herbivore-induced plant volatiles in numerous tritrophic systems elicit responses from predators and parasitoids (Dicke et al. 1990, Takabayashi and Dicke 1996). The induction signaling pathways appear to be general among plants, consisting of the Jasmonic Acid and Salicylic Acid pathways (Cipollini and Redman 1999, Dicke et al. 2003, Baldwin et al. 2006), and many plants produce some similar end products such as hexane, which are commonly referred to as green leaf volatiles (Baldwin et al. 2006, Gohole et al. 2003). However, there is also variation in the end product blend that sometimes allows predators and parasitoids to discriminate between species of plants (Lewis and Martin 1990, Gouinguene et al. 2001, Liu and Jiang 2003, Fritzsche Hoballah et al. 2002), species of herbivores (Blaakmeer et al. 1994, Lewis and Martin 1990, De Moraes et al. 1998, Dicke 1999), and even the age or density of herbivores (Dicke 1999, Takabayashi et al. 2000, Gouinguene et al. 2003). Induction signals have the potential to provide a great deal of information to predators, but they also have the potential to provide misleading information.

The utility of herbivore-induced volatiles for agricultural biological control has been debated in the literature (Bottrell et al. 1998, Degenhardt et al. 2003, Dicke et al. 1990). Some argue that artificially enhancing volatiles in the field will arrest parasitoids in the area, leading to better control, while others argue that artificially enhanced volatiles will produce misleading signals, reducing the receptiveness of parasitoids to volatiles. In a few field studies, artificially enhanced volatiles have led to higher parasitism, but it is unclear whether this is due to better attraction of parasitoids from outside the field, better

retention of parasitoids within the field, or increased efficiency of parasitoids within the field (Thaler 1999, James and Price 2004).

Research on the quality of volatile signals has looked at the specificity of volatile production (Blaakmeer et al. 2004, De Moraes et al. 1998, Dicke and Takabayashi 1991) and the parasitoid's ability to discriminate between odors (Agelopoulos and Keller 1994, Fritzsche Hoballah et al. 2002). However, being able to discriminate between volatiles does not mean that predators and parasitoids will respond to specific plant volatiles in the wild. Many parasitoids have the ability to learn new signals based on past experience (Lewis and Martin 1990, Kester and Barbosa 1991). Additionally, there is heritable variation in parasitoids for responding to plant volatiles (Lewis and Martin 1990, Wang et al. 2004). The proximate incentives for a parasitoid to learn to respond to a signal or for a population of parasitoids to evolve a response to a signal are the same- the induced volatiles must correlate in time and space with herbivore availability. When the volatiles are not consistently correlated with herbivore presence, there is incentive for parasitoids to maintain variation in this response, either through genetic variation or phenotypic plasticity (Wang et al. 2003). In studies where the volatile signal has been disconnected from the herbivore presence, such as by saturating fields with volatiles, parasitoid response to the signals has decreased (Lewis and Martin 1990).

Some work has been done to document the time course of induction in various systems (Gouinguene et al. 2001, Mattiacci et al. 2001, De Vos et al. 2005), but relating this time course to parasitoid efficiency has not been thoroughly investigated. Mattiacci et al. (2001) found that *Cotesia glomerata* responded to plants only after herbivores had been feeding for at least three days, but quit responding to plants if the herbivores had

been removed for more than one day. This indicated that the plant's lag to induce volatile production was longer than the lag to cease volatile production. However, Agelopoulos and Keller (1994) found that induced plants where the herbivores had been removed were just as attractive to *Cotesia rubecula* 22 hours after herbivore removal as immediately after removal. This leads to the question, which we address in this study: how long can a plant's lag time to volatile production be and still produce a relevant signal to the parasitoid?

There is very little work done on the spatial aspects of induction. While it has been shown that induction can cause attraction to plants within a wind tunnel type environment (Agelopoulos and Keller 1994) and that inducing plants can trigger arrestment in predators and parasitoids (Agelopouolos and Keller 1994, Jang et al. 2000), we have no record of the distances over which these induced cues may act in the field. Designing field experiments to test attraction to induced plants is a difficult task (Gross 1981). Identifying the point at which an insect switches from random movement to directed flight as well as identifying which environmental cues out of the complex volatile environment triggered the change, is a challenge that has yet to be successfully tackled in the field.

An alternative approach for looking at tritrophic systems is to use computer simulations to predict how parasitoids should respond to a complex environment (Dunning et al. 1995, Takagi 1999). This allows us to simultaneously test more variables than is possible in a laboratory setting while also affording us more control over parameters than is possible in field experiments. By artificially establishing patterns of

environmental parameters, we can identify which plant, herbivore, and predator behavioral combinations lead to the most successful parasitoid foraging.

In this paper we use the tritrophic system of *Cotesia rubecula*, *Pieris rapae*, and *Brassica oleracea* to ask how the temporal and spatial patterns of herbivore induced plant volatiles impact parasitoid foraging success. The extensive work on volatile signals in this system, as well as the extensive life history data available for these three species, makes this a useful tritrophic system for detailed simulation analysis. *Pieris rapae*, the cabbage white butterfly, is a cosmopolitan herbivore that feeds primarily on members of the Cruciferaceae family (Kaiser and Cardé 1992). While these plants generally share similar chemical defensive profiles (Kaiser and Cardé 1992, Geervliet et al. 1994), there is also considerable variation in form and distribution of the plants, and it has been shown that *P. rapae* prefers certain host types over others, even within the species *Brassica oleracea* (Jones and Ives 1979). *Cotesia rubecula* is a specialist parasitoid that can attack all stages of hosts, but which suffers greater mortality when attacking older hosts (van Driesche et al. 2003, Nealis 1990). It has been shown repeatedly to be responsive to herbivore-induced plant volatiles with positive experience reinforcing this response (Kaiser and Cardé 1992, Blaakmeer et al. 1994, Geervliet et al. 1994). *C. rubecula's* response to plant volatiles is so strong that it will respond multiple times even to plants after caterpillars have left (Nealis 1990), begging the question what advantage does a parasitoid gain from this response.

Methods

Initial Model Framework and Validation

While many of the biological assumptions made in the spatially-explicit simulation model described in this paper cannot be immediately tested empirically, it is possible to compare this model to a simpler stage-specific model described in Puente et al. (in prep) that modeled the same phenomena in a non-spatial, deterministic manner. By setting all initial parameters equal in the two models, we can verify that the initial programming is correct. Additionally, the deterministic model enables identification of appropriate parameter ranges for some variables in the stochastic model.

Over a daily time step, the following events occurred in the same order for both models: mortality of herbivore larvae, maturation of herbivore larvae (including removal of any larvae old enough to pupate), and new herbivore larval occupation of plants. Life table data for *P. rapae* were gathered from several sources (Jones et al. 1987, Parker 1970, Harcourt 1966a, Dempster 1967). Overall pre-adult mortality ranged from 69.1 to 95.9%. If the Harcourt data which included no egg parasitism are ignored, the average pre-adult mortality was 91.6% ± 1.1% s.d.; this is surprisingly consistent considering the variety of host plants and geographic regions these data were collected from. We chose to use the life table from Dempster (1967) because it is consistent with the majority of the published life tables and covered the herbivore's lifespan in more detail. The daily herbivore mortality rates used in both models can be seen in Table 1.

One major difference between the models is that mortality in the deterministic model was a fixed proportion applied to all plants occupied by the same larval cohort. In the current simulation model, the mortality rates used were the same as in the

deterministic model, but the probability of an individual larva dying was a stochastic process. A random number between 0 and 1 was selected by the computer (see Appendix for random number generator code), and if the number was less than the probability of mortality, the larva was "killed". In a large field, this process should produce roughly the same overall mortality rate as was found in the deterministic model.

The deterministic model defined the **occupation rate** as the proportion of plants receiving *new* larvae over one daily time step; occupation rate is not a measure of the total number of plants with larvae at any point in time. Because the deterministic model did not follow non-feeding stages such as eggs and pupae, when validating the model, the simulation began with occupation by first instar larvae, rather than oviposition of eggs. In the deterministic model, the proportion of plants receiving new larvae was a fixed fraction of each cohort of plants. In the current simulation model, the plants receiving new larvae were determined by a random number generator without regard to of their current induction or occupation state. To mimic the constraint in the deterministic model of only following one larva per plant, during the validation process of the current model, plants were only allowed to be occupied by one new larva per time step, and any previous larvae on the plant were removed when a new larva replaced them. Once the models were validated, these assumptions were removed to allow herbivores to start as eggs and to allow multiple eggs per plant. This allowed our simulation to reflect more realistic dynamics of *P. rapae*, especially at higher herbivore infestation levels.

Following occupation, plants were evaluated in each time step for initiating induction. The **induction delay**, or how many days a larva must feed on the plant before the plant begins volatile production, was varied from one to five days. In the model

validation process, if a larva had been at the age to induce the plant when it was removed by a new larva occupation of the plant, the plant would still be induced. Likewise, the **relaxation delay**, or how many days following abandonment by an inducing larva (through mortality, maturation, or replacement by a younger larva), was varied from one to five days. In the deterministic model, it was found that both induction delay and relaxation delay had an effect on signal relevance, but a change in induction delay had less of an impact on signal relevance than a change in relaxation delay.

In the deterministic model it was found that varying the oldest viable **host stage** a parasitoid is able to attack changed the value of signal relevance. Viable host stage has been shown to be an important parameter biologically. For example, *Cotesia glomerata* is unable to attack *P. rapae* larvae above the third instar because the hosts are able to encapsulate the parasitoid larvae at that stage, so there is higher parasitism on host plants that slow the growth of *P. rapae* larve (Benrey and Denno 1997); however, *C. glomerata* cannot identify the stage of an herbivore based on plant volatile cues (Mattiacci and Dicke 1995). In the model, when a parasitoid is only allowed to attack younger larvae, older larvae on the plant still induce the volatiles but the plant is classified as unoccupied from the parasitoid's point of view. We ran the model to consider cases where parasitoids could attack first instars only, first and second instars only, or all five instars.

To validate the current model, both models were run for 100 time steps before the proportion of plants falling into each major category was calculated. The deterministic model was run once and the simulation model was run twenty times and then averaged for each induction-relaxation delay combination and for occupation rates varying from

0.01 to 0.9. The value of signal relevance was calculated for both models using the formula described in Puente et al. (in prep).

One question when designing the simulated field of plants is what dimensions the field should be. While an infinitely large field, as assumed in the deterministic model, would allow the parasitoid more freedom of movement without encountering field boundaries, very large fields place a greater strain on computing resources and do not reflect the realities of a true field. The maximum number of hosts a parasitoid could attack in the deterministic model is limited by the time the parasitoid has to forage rather than the number of hosts in the field. Therefore, we could use the deterministic results to calculate the minimum field size needed in the stochastic model to make the parasitoids time limited rather than space limited. We used the following formulas, given the number of hosts attacked (N_A) and distribution of plants signaling and occupied (SO), not signaling and occupied (NO), not signaling and empty (NE), and signaling and empty (SE) from the deterministic model:

N_{Asig} = fieldsize * (SO/ (SO+NO+NE+SE))

N_{Aran} = fieldsize * ((SO + NO)/ (SO+NO+NE+SE))

We ran the deterministic model for induction delays of 1 to 5 days, relaxation delays of 1 to 5 days, occupation rates from 0.01 to 0.9, and viable host ranges from first to fifth instars. This allows us to estimate the minimum field size needed for the stochastic simulation.

For all parameter combinations explored, randomly foraging parasitoids were able to exhaust their time in fields with greater than 70 plants. Parasitoids foraging with signals needed much larger fields to exhaust their time budget (see Table 2). In about 80% of the parameter combinations, a field size of 400 plants was sufficient for the signal-foraging parasitoids. There were two conditions which required larger field sizes. First, in cases where the occupation rate was <0.02, the rarity of occupied plants led to even fewer signaling occupied plants, and thus a larger field was needed. Second, in cases where the occupation rate was large (e.g. 0.9), the viable hosts were young (first instars) and the induction delay was larger than the viable host stage (e.g. 4 days), because newer larvae always replaced older larvae, the proportion of plants that could maintain a larva long enough to induce the plants to signal was miniscule. In the first case, the minimum field size was close to 400; in the second case the minimum field size could get well above 10,000 plants, but because this was an artifact of a constraint in the deterministic model, we felt that a field size of 400 plants would be sufficient for the stochastic model once we removed the assumptions of the deterministic model.

Another question we hoped to answer by comparing the simulation to the deterministic model was how many simulation runs were sufficient for capturing the impacts of the parameters of interest, given the stochasticity of herbivore mortality and occupation. From the deterministic model, we found that varying induction delay, relaxation delay, occupation rate, and viable host stages could impact the values for signal relevance, so we tested the extreme values (induction and relaxation delays of either 1, 3, or 5 days; occupation rate of either 0.01 or 0.9; viable host stage of either first or fifth instars) in our stochastic model to see which parameters were most sensitive to

number of simulations run. We calculated the mean and standard error of the signal relevance and number of hosts attacked for both signal-following and randomly foraging parasitoids for each successive run, and determined how many runs were necessary for the standard error to fall within 5% and 10% of the mean.

The results of varying the number of runs for each set of parameters is found in Table 3. Under most circumstances the standard error was within 10% of the mean after fewer than five runs, and twenty runs were more than sufficient to reach a standard error within 5% of the mean for number of hosts attacked for signal-following parasitoids, number of hosts attacked for randomly-foraging parasitoids, and for overall signal relevance. The only exceptions were situations where the occupation rate was at the lowest value (0.01), and where the induction delay was greater than the development time for the viable host stage. In these cases, over a hundred runs were not sufficient to capture the variance. This was probably due to the presence of runs where no plants were signaling, thus weighting the mean with numerous zeros. This indicates that for most parameters, twenty runs will be sufficient, but more runs should be used for lower occupation rates.

Simulating Natural Herbivore Population Dynamics

In the stochastic simulation we were able to remove many of the unrealistic assumptions the deterministic model made about *P. rapae* population dynamics. The first major improvement was the ability to follow multiple larvae on a single plant, such that if the youngest larva died, but an older larva remained, the plant could remain induced and occupied. It has been found that *C. rubecula* is more responsive to plants hosting more larvae (Kaiser and Cardé 1992, Kaiser et al. 1994, Geervliet et al. 1998), so being able to

follow multiple larvae opens up the possibility of simulating a change in volatile strength due to the herbivore load on a particular plant. We designed our model to follow up to twenty herbivores on a single plant. To see the effect following multiple larvae had on the distribution of plant states, we compared the proportion of plants actually occupied ((NO+SO)/ (NO+SO+SE+NE)) over a range of occupation rates (0.01 to 0.9) assuming all five instars were viable host stages, for the deterministic assumption of single occupation and the more realistic assumption of multiple occupations. At occupation rates < 0.05, allowing multiple larvae per plant does not change the overall proportion of plants occupied; however, at above this occupation rate, there were significantly more plants occupied in the multiple larvae case (see Figure 1) . While in the deterministic model, occupation never reached 100%, by allowing multiple larvae, the stochastic simulation can reach 100% occupation at a daily occupation rate as low as 0.6.

The deterministic model was only able to follow larvae, but in the stochastic simulation we are also able to follow eggs, pupae, and adults. While the presence of eggs and pupae do not impact the plant's induction state directly, the source of egg mortality could change the proportion of plants actually occupied and could affect the time course of the field dynamics. Following pupae also allows us to follow the herbivores over multiple generations because we can continuously track all individuals. To see the effect including eggs and pupae had on the distribution of plant states, we compared the proportion of plants actually occupied ((NO+SO)/ (NO+SO+SE+NE)) over a range of occupation rates (0.01 to 0.9) assuming all five instars were viable host stages. Adding egg and pupal stages reduces the overall proportion of plants occupied due to the added mortality, especially in the egg stage (see Figure 1). When egg mortality is included, the

simulation model matches the deterministic model up to an occupation rate of 0.1, and occupation does not reach 100% until an occupation rate of 0.7.

To simulate oviposition dynamics, we had to follow adult dynamics as well as larval dynamics. After eight days, eclosing pupae were placed in a new adult class. Richards (1940) found that adult *P. rapae* populations usually had a 1:1 sex ratio; therefore, the new adult class was divided in half to account for males (which do not oviposit), before being added to the rest of the adults in the population. Adult *P. rapae* live for about three weeks (Harcourt 1963), so for each daily time step the number of adults was reduced by the number of new adults 21 days prior to that time step. No other adult mortality was considered.

Because the stochastic simulation follows individual plants, the spatial relationship between plants can be studied in this model. *P. rapae* are disproportionately aggregated at the edges of fields (Courtney 1986, Harcourt 1966b, Harcourt 1963). This is primarily due to the movement patterns of adult butterflies, which has been studied extensively (e.g. Jones 1977, Root and Kareiva 1984, Fahrig and Paloheimo 1988, Lee and Heimpel 2005). We based our herbivore distribution on an algorithm developed by Jones (1977) to recreate *P. rapae's* spatial distributions. In natural populations, butterflies were observed to fly in a roughly straight path (Jones 1977, Root and Kareiva 1984), but not necessarily in the same direction as other butterflies in the field (Fahrig and Paloheimo 1988, Root and Kareiva 1984). In the model, each adult was given a starting position and a directional bias at random. The adults either remained at their current location for a time step with a probability of 0.32 (Jones 1977) or moved forward by a single unit, either in the direction of their bias with a probability of 0.2, to either side of

their directional bias with a probability of 0.175, orthogonal to their bias with a probability of 0.125, opposite and to the side of their bias with a probability of 0.075, or opposite their bias with a probability of 0.05 (see Figure 2). The probabilities for these movements were based on turning radius studies by Root and Kareiva (1984). Following movement, the probability that the adult would oviposit was 0.23, the median probability found by Jones (1977). Field observations found that butterflies crossed patch boundaries without stopping (Root and Kareiva 1984, Lee and Heimpel 2005). In order to reflect this and maintain the same field densities, adults reaching the edges of the simulated field were 'mirrored' to the opposite side of the field (Bukovinszky et al. 2005). Adults continued to follow this algorithm until they had laid a set number of new eggs. To prevent butterflies remaining indefinitely in a field that had reached its capacity of eggs and larvae, when butterflies encountered ten plants that were fully occupied, they left the field.

We wanted herbivore populations to reflect natural population sizes, so we set the initial adult population size to 1, included adult dynamics, and varied the number of eggs each butterfly could lay per day. We averaged the number of eggs, larvae, and adults for five runs lasting 100 days for each of the following oviposition rates: 1, 2, 5, 10, 15, and 20 eggs/butterfly/day. We then compared the average values to reported field densities, correcting for field size. The density of eggs observed in Parker (1970) was higher than any values we ran, but the densities observed in Jones et al. (1987) were approximated relatively well by either 15 or 20 eggs/butterfly/day, especially in the second and third generations (Fig 3a). The first larval instar densities observed by van Driesche (1988) in kale were closely approximated by 10 eggs/butterfly/day, while the first larval instar

densities observed by van Driesche and Bellows (1988) in collards were approximated by the second generation of simulations for 15 or 20 eggs/butterfly/day (an offset of about 30 days) (Fig 3b). The number of adults in the field observed by van Driesche (1988) was similar to the results of 10 eggs/butterfly/day (Fig 3c). Therefore, for the remainder of the experiments, "low herbivore density" means 10 eggs/butterfly/day and "high herbivore density" means 20 eggs/butterfly/day.

Parasitoid Foraging Algorithms

The questions we wanted to answer by simulating parasitoid foraging paths included:

- How does underlying host distribution and plant signaling distribution impact the number of host attacks by foraging parasitoids?
- How does parasitoid sensitivity to odor concentration impact the effectiveness of host signals?

Numerous environmental factors can influence parasitoid foraging efficiency such as wind speed (Keller 1990, Elzen et al. 1987), light intensity (Elzen et al. 1987), or previous experience (Keller 1990, Kaiser and Cardé 1992, Geervliet et al. 1998). While these can be important, they are beyond the scope of this paper.

We assumed the following constants for both randomly foraging and selectively foraging parasitoids. Sato and Ohsaki (2004) observed that for *C. glomerata* searching for *Pieris* larvae, the time spent searching one leaf was 73.5 ± 11.9 seconds, so this was used as the time spent in fruitless search if the parasitoid arrived on a plant with no host ("c" in

the deterministic model). There is some evidence that *C. glomerata* avoids superparasitizing already parasitized larvae (Fatouros et al. 2005), so a parasitized larva was considered "non-host" but was still capable of inducing a plant. We assumed a parasitoid would be equally likely to find a host early or late in that search time interval so on average a parasitoid would spend half as much time searching if it encountered a host on that plant. Although there are circumstances that would prevent parasitoids from discovering available hosts (e.g. plant architecture - Andow and Prokrym 1990), we assumed that if a viable host was available, the parasitoid would find it. The time it took for a parasitoid to successfully sting a host ("b" in the deterministic model) was 13.1 ± 3.9 seconds (Sato and Ohsaki 2004). The recorded flight speed for *C. rubecula*, a closely related species that also parasitizes *P. rapae*, was 0.33 m/second (Kaiser et al. 1994). And plants were assumed to be placed on a grid, one meter between each plant.

Parasitoids were given 3600 seconds of total foraging time. Although the exact amount of time real parasitoids spend foraging in the field is unknown, one hour per day was considered a reasonable estimate given that most parasitoids only forage during the brightest hours of daylight and must divide time between foraging for food and foraging for hosts (Bartlett 1964). A parasitoid started its foraging location in the field randomly selected by the simulation model, and immediately searched the plant it was on. If no viable host was present, the giving-up time was discounted from the total foraging time and the parasitoid moved to the next plant. If a viable host was present, the host was marked as parasitized, the handling time was discounted from the total foraging time, and half the giving-up time was discounted from the total foraging time to account for search time. After successfully parasitizing a host, parasitoids remained on the plant to continue

searching with a probability of 0.33 (Tenhumberg et al. 2001). In wind tunnel experiments, the presence and concentration of host odors did not affect *Cotesia rubecula*'s flight speed or direction of travel, but did impact a parasitoid's willingness to take off and whether a parasitoid completed a flight (Kaiser et al. 1994, Keller 1990); therefore we felt that the above flight parameters could be used equally for both randomly and selectively foraging parasitoids.

The spatial aspects of parasitoid foraging are very poorly understood, so we had to make many assumptions in this part of the model. The following assumptions we believe to be reasonable:

- Plant volatiles dilute over space, so a parasitoid is more likely to detect a closer plant than a farther plant.
- Parasitoids use volatiles to detect a potential host plant, even if they are not *herbivore-induced plant volatiles*, so randomly foraging parasitoids are also more likely to detect a closer plant than a farther plant. (Nordlund et al. 1988)
- Parasitoids decide which plant they will fly to before they leave the plant they are on. (Keller 1990)

To determine which plant a parasitoid would move to next, we picked randomly from a list of all possible plants weighted according to their distance from the parasitoid's current position (hereafter called the "picking list"). We assumed a maximum flight distance of five meters per single move to get a list of all sixty possible moves a parasitoid can make each time it leaves a plant (Table 4). For each possible move we took the parasitoid's current location and added the column value and the row value multiplied by the number of plants per row to get a plant number. If the plant number was greater

than the total number of plants in the field, we subtracted the total number of plants in the field to send it back to the first row. If the plant number was less than zero, we added the total number of plants in the field to send it to the top row. This created a field with wrap-around borders.

Once we calculated a plant number, we used its distance to determine how many times we added it to the picking list. For example, if a plant was one meter away from the parasitoid's location, and the bias for a plant one meter away was five, the plant was added to the picking list five times. We used two different forms of bias: linear and exponential. According to Elkinton et al. (1984), over short distances, volatile such as pheromone plumes spread out in a linear fashion, therefore one bias was "Linear". We assumed that the strength of signal had a value of one at the distance of one meter and zero at a distance of six meters and then used a basic linear equation to predict what the signal value was for intermediate values (Table 5, Linear Diffusion). This created a bias where a parasitoid was five times as likely to go to a plant one meter away compared to a plant five meters away.

The other form of bias we assumed was an exponential diffusion. In diffusion models where plumes are not as well delineated, decay of volatile concentrations happens at a rate relative to the inverse of the radius squared (Murlis et al. 2000). We calculated what one divided by distance squared was for one to five meters. (Table 5, Exponential Diffusion: Expected). We then divided each of these values by the smallest value to get a relative value, and rounded this value to get a bias (Table 5, Exponential Diffusion: Bias). This created a bias where a parasitoid was twenty-five times as likely to go to a plant one meter away compared to a plant five meters away. Although it is likely that the actual

spatial dynamics of detection distances is not either of these two options, we felt this would be adequate for looking at the sensitivity of the model to a parasitoid's odor detection bias.

Additionally, we wanted to prevent a parasitoid from immediately returning to the plant it came from. As the picking list was created, "total number of plants in the field + 1" was put in place of the plant the parasitoid immediately came from. Once the picking list was completely filled, we picked a random number between one and the size of the picking list to select which plant the parasitoid flies to next.

In the case of following herbivore-induced volatiles, the following change to the algorithm was made. When the plant number was calculated, the plant's induction status was checked. If the plant was not induced, instead of adding the plant number to the picking list, a value outside the field size (total number of plants in the field + 1) was added to the list. Once the picking list was made, it was inspected by the computer algorithm, and as long as at least some value was within the field, random numbers were drawn until that number matched with a list position of a plant number inside the field. If none of the plants on the picking list were within the field (i.e. no inducing plants within range) then the picking list was remade using the random movement algorithm and the parasitoid moved to a random non-induced plant.

A summary of the variables and constants used in this simulation can be found in Table 6.

Results

We examined time series of the mean number of herbivores attacked by parasitoids randomly foraging and by parasitoids following signals, for both linear and

exponential distance biases, for every combination of parameters we considered. In all parameter combinations we tested, the mean number of hosts attacked by randomly foraging parasitoids with linear biases was within one standard deviation of the mean number of hosts attacked by randomly foraging parasitoids with exponential biases. Averaging over all parameter combinations, parasitoids randomly foraging visited about eight more plants per day than parasitoids following signals (Table 7), regardless of parasitoid distance bias. By looking at the difference in mean number of larvae attacked for each five-day sampling interval for parasitoids following signals versus parasitoids randomly foraging, each of our combinations of induction delays, relaxation delays, herbivore densities, and viable host stages could be classified as one of four patterns:

A. Following signals was on average disadvantageous, but individual runs could be advantageous due to large variances,
B. Following signals was no better or worse than randomly foraging for any time interval sampled,
C. Following signals was advantageous for at least one host generation, as long as the parasitoid flight bias was linear,
D. Following signals was advantageous for at least one host generation, regardless of parasitoid flight bias.

In pattern A, parasitoids following signals generally attacked as many hosts as parasitoids not following signals through the first two generations of herbivores, but fell much lower in the third generation (e.g. see Figure 4a). Of the 54 parameter combinations we tested, six combinations fell into this pattern. The most extreme loss of attacks by parasitoids following signals over a season was 76.6 hosts, under the conditions of a five

day induction, five day relaxation, low herbivore density, only first instars as viable hosts, and an exponential distance bias. In these simulations the variance of hosts attacked in the third generation of herbivores was quite large such that the mean for parasitoids randomly searching was well within a single standard deviation of the parasitoids following signals. This first pattern was only seen when the induction delay was greater than one and the oldest viable hosts were either first or second instars.

In pattern B, parasitoids following signals generally attacked as many hosts as parasitoids not following signals throughout the year (e.g. see Figure 4b). Over a season, this could result in a net loss of up to 42 hosts or a net gain of up to 75 hosts, but for any day sampled the means for number of hosts attacked if the parasitoids followed signals were well within a standard deviation of the means for number attacked if the parasitoids foraged randomly. Of the 54 combinations we tested, twelve combinations fell into this pattern, all of which had an oldest viable host stage of either first or second instars. In almost all of these cases, the induction delay was 5 days; the only exception being two cases where the induction delay was 3 days and only first instars were attacked. In all of these cases, the signals were produced after the inducing host has matured beyond the viable attack stages; therefore, it is not surprising that the resulting host attack rates for parasitoids following signals should not be significantly different from randomly foraging parasitoids.

In pattern C, there was a clear effect of parasitoid flight bias in the first generation (see Figure 4c). For parasitoids with a linear distance bias, the gain in hosts attacked ranged from 16.2 to 167 hosts over a whole season. For these same conditions, parasitoids with an exponential distance bias, the difference between the signal foraging

parasitoids and the randomly foraging parasitoids over a whole season ranged from a loss of 40 hosts to a gain of 78 hosts. Pattern C occurred in five of the 54 combinations, all of which had first and second instars as viable hosts and an induction delay of either 1 or 3. Because this advantage was only apparent in the first generation when hosts are rare in the field, it is likely that a linear bias allowing parasitoids to move greater distances between plants allowed parasitoids to encounter more patches of viable hosts, and a well synchronized induction then led to the parasitoids remaining in the patch of viable hosts. Randomly foraging parasitoids with a linear bias were just as likely to leave a patch of viable hosts as they were to enter a patch, and signal foraging parasitoids with exponential biases were less likely to encounter a patch.

The remaining thirty-one parameter combinations fell into pattern D, where parasitoids following signals attacked more hosts than randomly foraging parasitoids, regardless of parasitoid distance bias (see Figure 4d). The advantage primarily occurred in the first herbivore generation, but sometimes extended into the second generation. By the third generation, there were sufficiently dense populations of hosts that parasitoids were reaching their saturation point regardless of their foraging strategy, as can be seen by the small standard deviations from day 80 onward. If all five instars were viable hosts, parasitoids always benefited from following signals. When only first instars were viable hosts, pattern D only occurred when the induction delay was 1 day. When second instars were the oldest viable hosts, if the host density was high and the induction delay was 1 or 3 days, pattern D occurred, but when host densities were low, pattern C occurred.

A summary of all simulations can be found in Tables 8 and 9. Although relaxation delay did not impact qualitatively which pattern a simulation fell into, the relaxation

delay did impact the total gain in hosts over a season. For example, in the case where all five instars were viable hosts, induction delay was five days, and host density was high, if the relaxation delay was 1 day, the parasitoids following signals could attack on average 109 more hosts per season compared to randomly foraging parasitoids; if the relaxation delay was 3 days, this gain was reduced to 79 hosts, and if the relaxation delay was 5 days, this gain was reduced to 77 hosts.

Discussion

Our model found that herbivore-induced volatiles can be both better and worse for the foraging parasitoid, depending on the synchrony of volatiles and herbivores. In the majority of parameter combinations, following herbivore-induced plant volatiles was a beneficial strategy for parasitoids. However, there were conditions that made this strategy less efficient for the parasitoids.

We found that induction delay is very important. Plants with patterns A and B, where signals were irrelevant or possibly detrimental to the parasitoids, tended to have an induction delay of three or five days. Relaxation delay was also important for determining the magnitude of effect following signals could have on parasitoids. These results differ slightly from the deterministic model, where relaxation delay was more important in determining relevance when populations were allowed to reach an equilibrium state. Both models show that understanding the molecular mechanism for inducing signals will be important for engineering volatile producing plants that optimize parasitoid foraging efficiency. Future work in the *Pieris rapae* system can test our prediction by looking at the natural variation of plant induction responsiveness and parasitoid preference. We predict that *Cotesia rubecula* should have a preference for

varieties of *Brassica oleraceae* that can begin volatile production within a day of herbivory onset and cease volatile production within a day of the herbivory ceasing.

Our model shows that how parasitoids perceive volatiles in space can be important for determining whether or not a parasitoid gains an advantage by following signals. Volatiles are considered important cues for "long-distance" foraging (Geervliet et al. 1998), but what constitutes "long-distance" is not clear in the literature. If this means that parasitoids can detect signals one meter away, that would be comparable to our exponential bias where parasitoids were 25 times more likely to visit a plant one meter away compared to a plant five meters away; in this case, parasitoids gained nothing from following signals in several cases. However, if parasitoids can detect signals and respond to signals from five times that distance away, such as in our linear bias example, signals were important for parasitoid foraging success. While this differentiation (pattern C) only occurred in five cases, these cases all occurred in simulations where second instars were the oldest viable host stage, which is biologically relevant for *Cotesia rubecula*, and occurred in the low herbivore density cases, which would be the desirable state for an agricultural setting. Because of the potential likelihood of these parameter conditions occurring in nature, understanding the mechanics of how volatile plumes disperse in space and how parasitoids perceive these volatiles in space could be very important for knowing whether breeding for inducing plants will be a successful endeavor.

Finally our model shows the importance of underlying herbivore densities for the relevance of volatile cues. In the first herbivore generation, when the number of herbivores was at its lowest (Figure 3b), signals had the greatest impact (Figures 4c and 4d). In the third generation, when herbivores were at their highest densities, signals were

irrelevant. This pattern is seen in biological control in general, where at low herbivore densities biological control can be effective at suppressing the population, but under outbreak conditions, biological control is not as effective (Murdoch and Briggs 1996). Most studies of induced volatiles examine just a single volatile source, which misses the potential importance underlying herbivore densities can have on parasitoid foraging success. Our model argues for looking at larger populations of plants and herbivores before determining whether a volatile signal is in fact relevant to parasitoids. We also argue that if breeding plants for volatile production is going to be a successful strategy, the volatile production needs to be produced early in the season, by young plants, if it is to improve parasitoid foraging efficiency.

While our simulation model has identified many important parameters that should be studied more closely, there are several modifications that future models could try to improve the spatial and temporal value of this model. One assumption we made in this model is that parasitoids are either foraging randomly or foraging in response to signals. We did not allow for parasitoids to change strategies within a lifetime. Other models have shown that evolving parasitoid systems can change host-parasitoid dynamics (Abrams and Kawecki 1999), therefore incorporating parasitoid learning into this model would be an important next step.

We specifically chose to focus on a naïve parasitoid entering a field of unparasitized larvae, rather than following an entire parasitoid population's dynamics over a season. Following parasitoid population dynamics would be an interesting extension for this model, but would require that considerably more parameters be estimated. Parasitoid and host eclosion are not always synchronized in nature (van der

Meijden and Klinkhamer 2000), parasitized herbivores can consume different amounts of foods than their non-parasitized congeners (Fatouros et al 2005, van Loon et al 2001, Horikoshi et al. 1997), and parasitized larvae can have different mortality than non-parasitized larvae (Jones 1987). These factors may all alter the relevance of volatiles in host plants over several generations. In many cases, less efficient individual predators or parasitoids will lead to more stable population dynamics over longer periods of time (Karimzadeh et al. 2004, van der Meijden and Klinkhamer 2000); therefore following long term dynamics could lead to different conclusions.

We framed our research question from the naive parasitoid's perspective- when should a parasitoid ignore the signal coming from plants? This question could also be framed from the plant's perspective- how accurate does a plant need to be, in order to attract parasitoids? However, this implies that parasitoids can exert a positive evolutionary pressure on the plants' fitness. There is some evidence that parasitized *Pieris* species consume less and therefore the plant can gain by recruiting parasitoids (Fatouros et al 2005), but it is possible that parasitism has no effect on plant fitness at all (Coleman et al. 1999), making the question from the plant's point of view inconclusive at best (Janssen et al. 2002). To make this model into an evolutionary argument, however, long term plant fitness should be included.

We hope this model will stimulate future research into the timing and spatial dynamics of herbivore-induced plant volatiles. While these are difficult parameters to measure in natural systems, they appear to be ecologically relevant, and therefore are important aspects to study, especially if this phenomenon is to be practically applied in agriculture.

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Table 1. Life Table for *Pieris rapae*

Stage	Day	Mortality	Mortality (Deterministic)
Egg	1	0.0235	0
	2	0.0235	0
	3	0.0235	0
	4	0.0235	0
	5	0.0235	0
1st instar	6	0.1872	0.1872
	7	0.1872	0.1872
	8	0.1872	0.1872
2nd instar	9	0.0874	0.0874
	10	0.0874	0.0874
	11	0.0874	0.0874
3rd instar	12	0.0842	0.0842
	13	0.0842	0.0842
	14	0.0842	0.0842
4th instar	15	0.1373	0.1373
	16	0.1373	0.1373
	17	0.1373	0.1373
5th instr	18	0.2331	0.2331
	19	0.2331	0.2331
	20	0.2331	0.2331
Pupae	21	0.0074	0
	22	0.0074	0
	23	0.0074	0
	24	0.0074	0
	25	0.0074	0
	26	0.0074	0
	27	0.0074	0
	28	0.0074	0

Table 2. Minimum Field Size Required (in number of plants)

	Mean	**Median**	**Max**	**Min**
Signal	446	172	16223	62
Random	57	57	67	47

Table 3. Minimum Number of Runs Required to Account for Variance in Herbivore Mortality

Initial Conditions				# of Runs for SEM < 0.10 * Mean			# of Runs for SEM < 0.05 * Mean		
Host Stage	**Induction**	**Relaxation**	**Occupation**	**N Signal**	**N Random**	**Relevance**	**N Signal**	**N Random**	**Relevance**
1	1	1	0.01	8	< 5	< 5	24	8	15
1	1	1	0.5	< 5	< 5	< 5	< 5	< 5	< 5
1	1	1	0.9	< 5	< 5	< 5	< 5	< 5	< 5
5	1	1	0.01	< 5	< 5	< 5	< 5	13	7
5	1	1	0.9	< 5	< 5	< 5	< 5	< 5	< 5
1	3	3	0.01	> 100	< 5	> 100	> 100	7	> 100
1	3	3	0.9	< 5	< 5	< 5	< 5	< 5	< 5
5	3	3	0.01	< 5	< 5	< 5	13	< 5	8
5	3	3	0.9	< 5	< 5	< 5	< 5	< 5	< 5
1	5	5	0.01	> 100	< 5	> 100	> 100	12	> 100
1	5	5	0.9	34	< 5	33	> 100	< 5	> 100
5	5	5	0.01	< 5	< 5	< 5	8	10	12
5	5	5	0.9	25	< 5	28	> 100	< 5	> 100

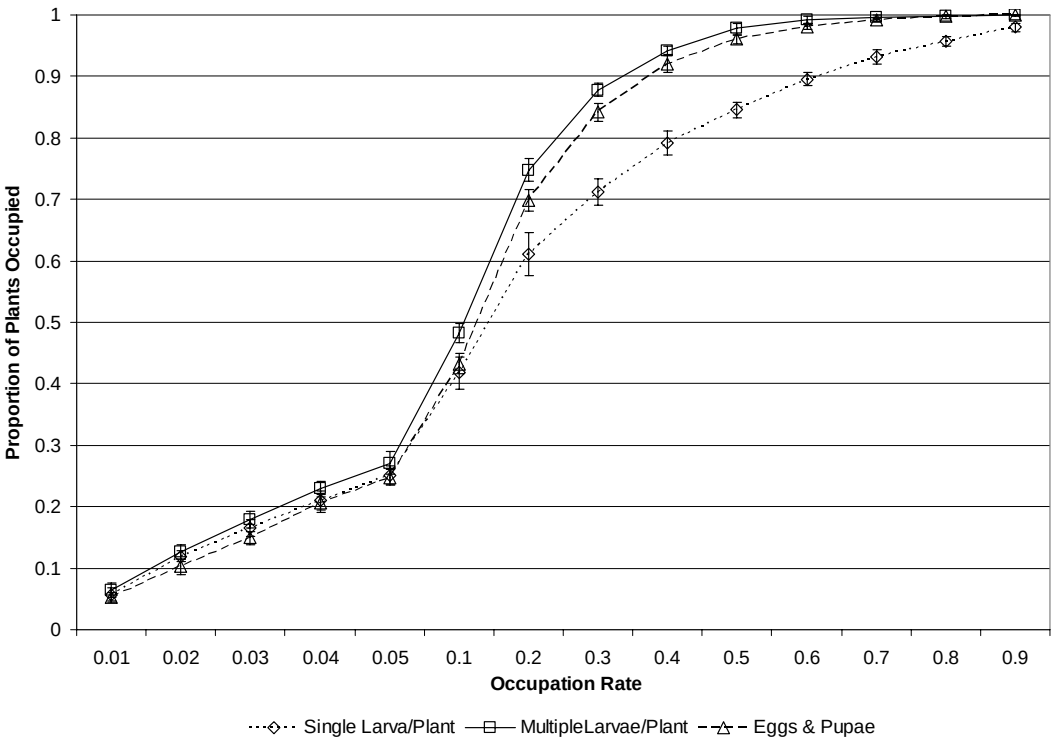


Figure 1. Effect of Assumptions on Herbivore Field Density. Single Larva/Plant is the result of the stochastic model matching the assumptions of the deterministic model, with only a single larva followed per plant. Multiple Larvae/Plant follows multiple larvae per plant in the stochastic simulation model. The Eggs & Pupae follow multiple larvae as well as eggs and pupae on each plant. Error bars indicate ±1 standard deviation.

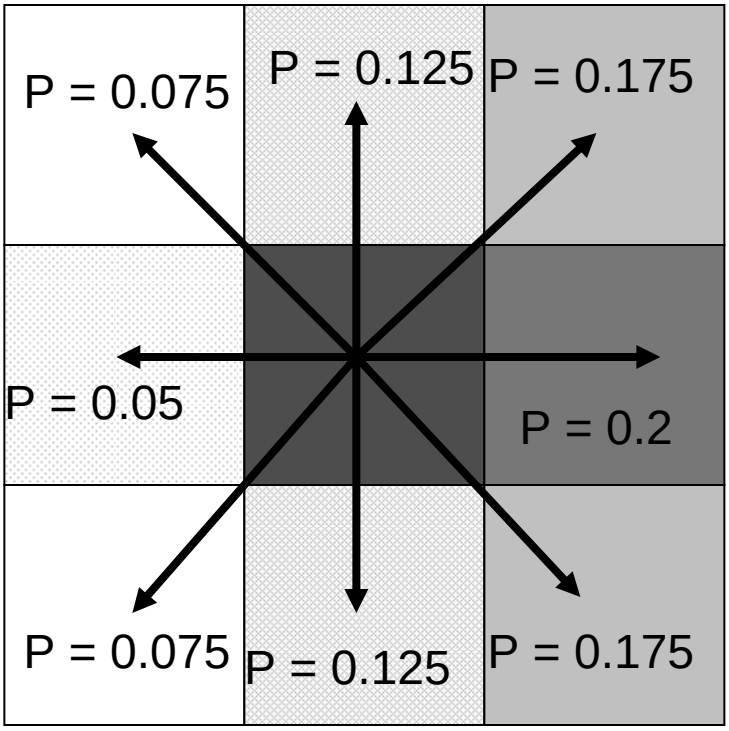
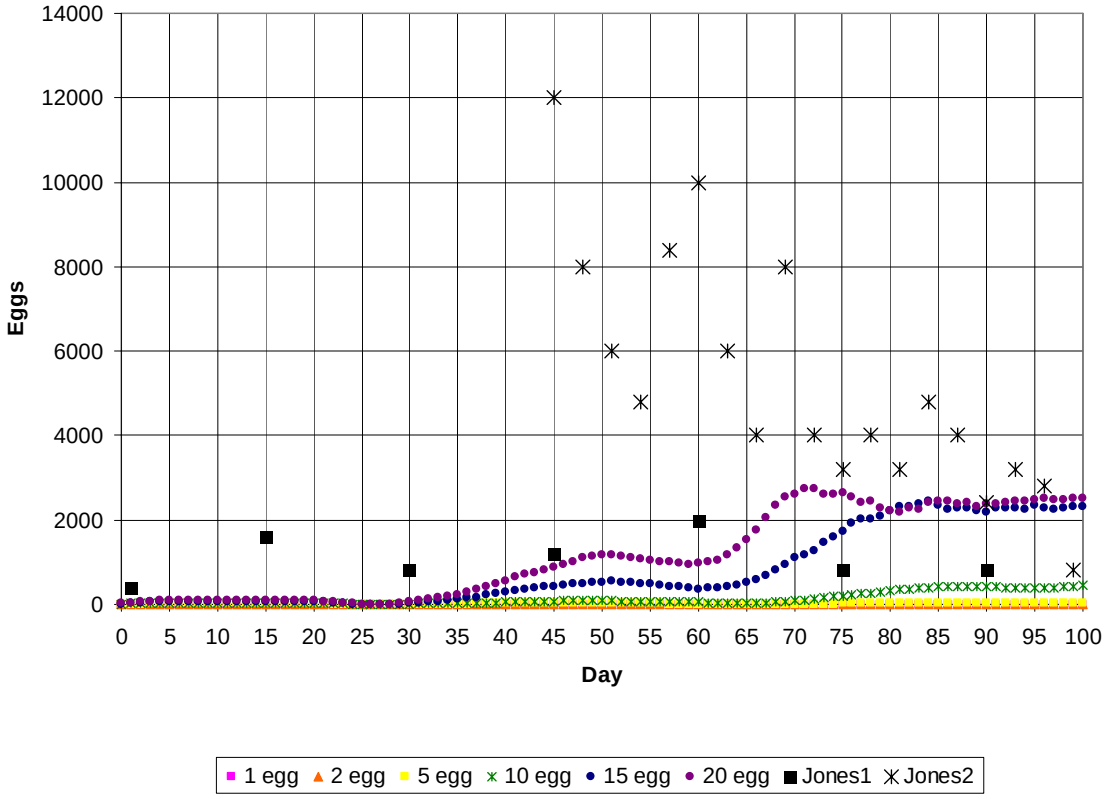


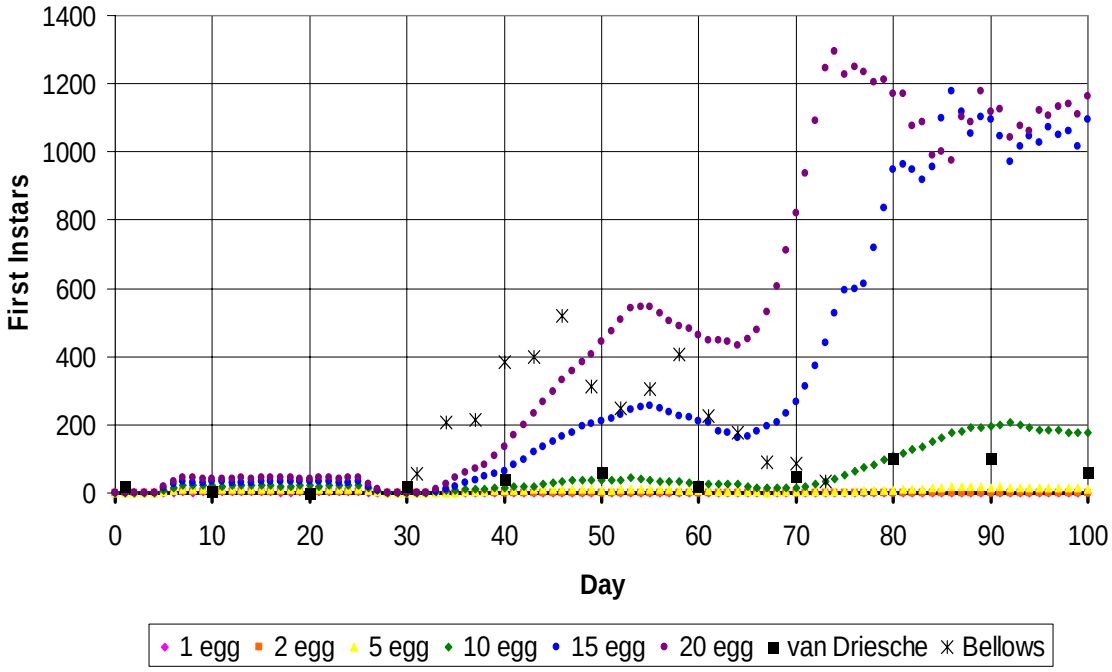
Figure 2. Spatial bias for *Pieris rapae* butterflies. Assuming a butterfly begins on a plant in the center square and has a bias to the right, the probability that a butterfly will travel to each square is shown by the p value in that square.

Figure 3. Comparison of Simulated Herbivore Population Dynamics with Published Field Data. The larger black symbols are data obtained from published studies, adjusted to match the size of our simulated field (400 plants). The numbers in the legend refer to the number of eggs each female butterfly would lay per day. a) Comparison of *Pieris rapae* egg densities. b) Comparison of *Pieris rapae* first instar densities. c) Comparison of *Pieris rapae* adult densities.

3a.


14000
12000
10000
8000
6000
4000
2000
0
Eggs
0 5 10 15 20 25 30 35 40 45 50 55 60 65 70 75 80 85 90 95 100
Day
1 egg
2 egg
5 egg
10 egg
15 egg
20 egg
Jones1
Jones2

3b.


First Instars
1400
1200
1000
800
600
400
200
0
0
10
20
30
40
50
60
70
80
90
100
Day
1 egg
2 egg
5 egg
10 egg
15 egg
20 egg
van Driesche
Bellows

3c.

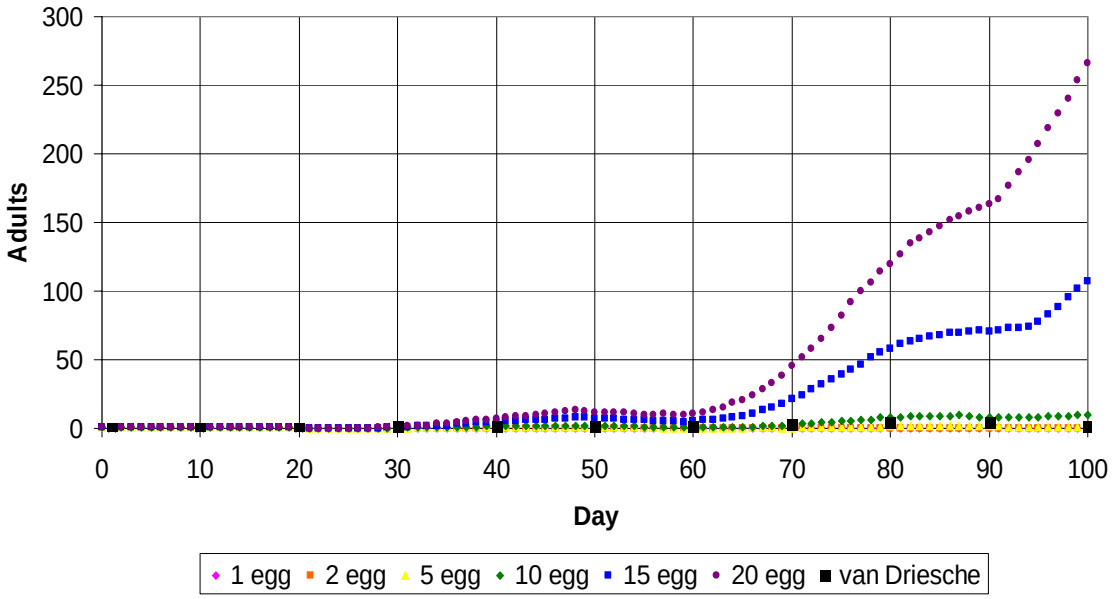

300
250
200
150
100
50
0
Adults
0
10
20
30
40
50
60
70
80
90
100
Day
1 egg
2 egg
5 egg
10 egg
15 egg
20 egg
van Driesche

Table 4. All Possible Moves for a Fixed Distance

Distance = 1		Distance = 2		Distance = 3		Distance = 4		Distance = 5	
row	column	row	column	row	column	row	column	row	column
-1	0	-2	0	-3	0	-4	0	-5	0
0	-1	-1	-1	-2	-1	-3	-1	-4	-1
0	1	-1	1	-2	1	-3	1	-4	1
1	0	0	-2	-1	-2	-2	-2	-3	-2
		0	2	-1	2	-2	2	-3	2
		1	-1	0	-3	-1	-3	-2	-3
		1	1	0	3	-1	3	-2	3
		2	0	1	-2	0	-4	-1	-4
				1	2	0	4	-1	4
				2	-1	1	-3	0	-5
				2	1	1	3	0	5
				3	0	2	-2	1	-4
						2	2	1	4
						3	-1	2	-3
						3	1	2	3
						4	0	3	-2
								3	2
								4	-1
								4	1
								5	0

Table 5. Distance Biases

	Linear		Exponential		
Distance	**Expected**	**Bias**	**Expected**	**Relative**	**Bias**
1	1	5	1	25	25
2	0.8	4	0.25	6.25	6
3	0.6	3	0.111111	2.777778	3
4	0.4	2	0.0625	1.5625	2
5	0.2	1	0.04	1	1

Table 6. Parameters used in the model

Parameter	Values
(Oldest Viable) **Host Stage**	1, 2, 5
Induction Delay (in days)	1, 3, 5
Relaxation Delay (in days)	1, 3, 5
Occupation Rate (in eggs/plants/field)[1]	0.1 - 0.9
Herbivore Density (in eggs/butterfly/day)	Low (10), High (20)
Total Foraging Time (T_t) (in sec)	3600
Flight Speed (a) (in m/sec)	0.33
Handling Time (b) (in sec/host)	13.1
Giving-up Time (c) (in sec/plant)	73.5
Foraging Style	Random, Signal Following
Distance Bias[2]	Linear, Exponential

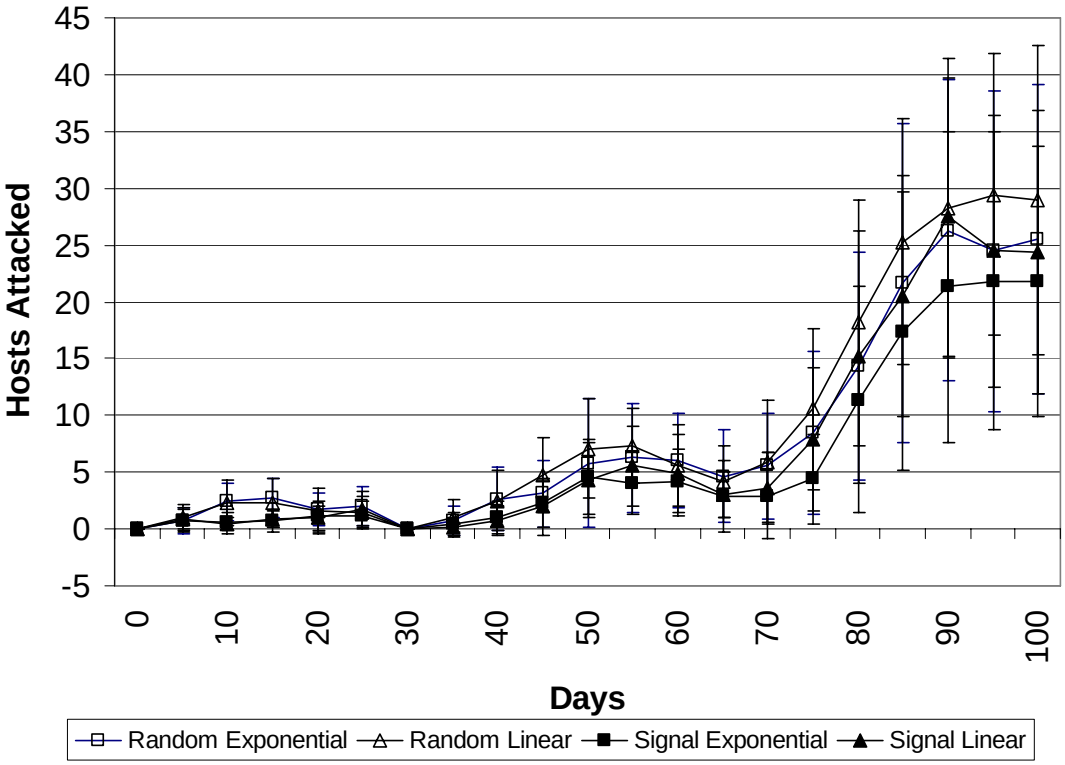
1. Occupation Rate was used solely in validating the model; for actual runs, Herbivore Density values were used. 2. Distance Bias is more thoroughly explained in Table 5.

Table 7. Average Number of Unique Plants Visited Per Day

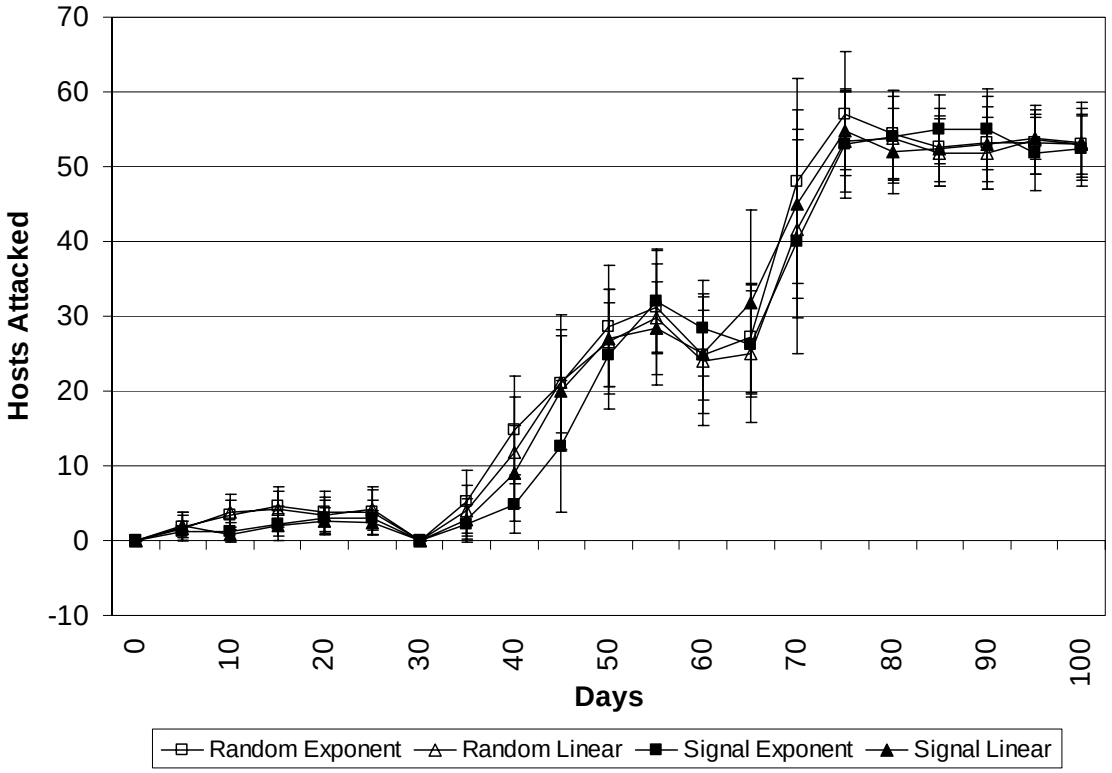
	Linear Bias	**Exponential Bias**
Follows Signals	32.6	32.5
Random	41.4	40.5

Figure 4. Time Series of Parasitoid Attack Rates. a) Detrimental signals (Pattern A); shown here is the case where induction delay is 3 days, relaxation delay is 3 days, herbivore density is low, and viable host stage is first instars only. b) Signals no better or worse (Pattern B); shown here is the case where induction delay is 5 days, relaxation delay is 5 days, herbivore density is high, and viable host stage is first instars only. c) Signals beneficial as long as the parasitoid distance bias is linear (Pattern C); shown here is the case where induction delay is 1 day, relaxation delay is 1 day, herbivore density is low, and viable host stages are second and first instars. d) Signals beneficial (Pattern D); shown here is the case where induction delay is 1 day, relaxation delay is 1 day, herbivore density is high, and all instars are viable host stages. For all four graphs, error bars are ±1 s.d.

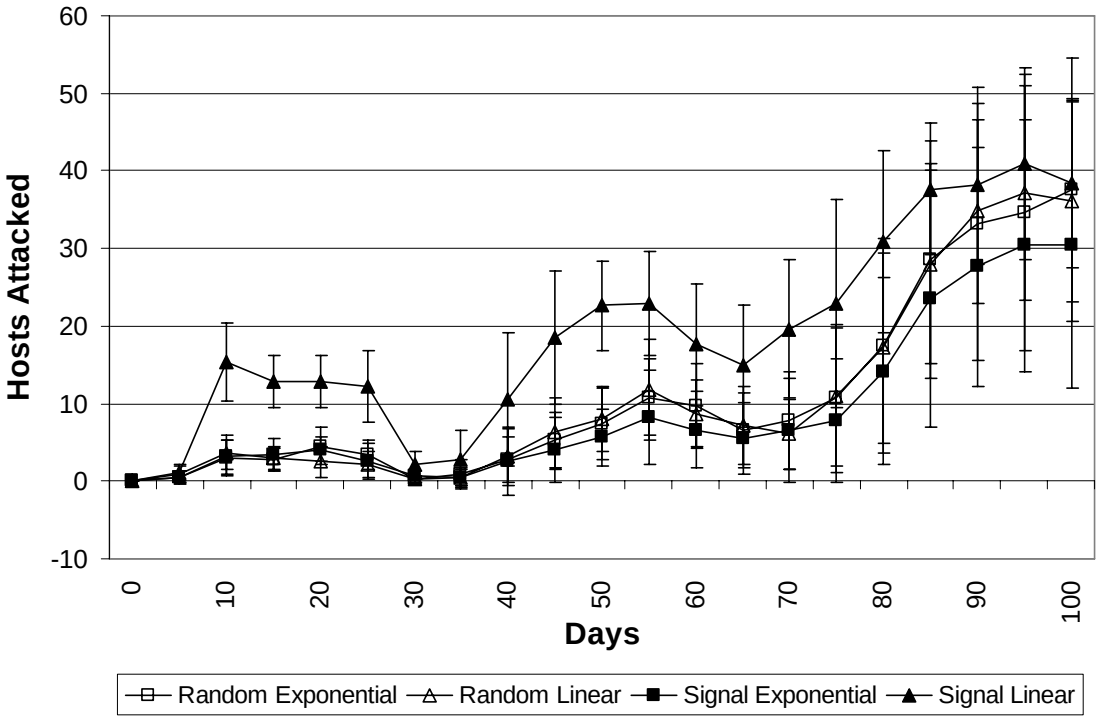
4a.


Hosts Attacked
45
40
35
30
25
20
15
10
5
0
-5
0
10
20
30
40
50
60
70
80
90
100
Days
Random Exponential
Random Linear
Signal Exponential
Signal Linear

4b.


70
60
50
40
30
20
10
0
-10
Hosts Attacked
0
10
20
30
40
50
60
70
80
90
100
Days
Random Exponent
Random Linear
Signal Exponent
Signal Linear

4c.


Hosts Attacked
60
50
40
30
20
10
0
-10
0
10
20
30
40
50
60
70
80
90
100
Days
Random Exponential
Random Linear
Signal Exponential
Signal Linear

4d.

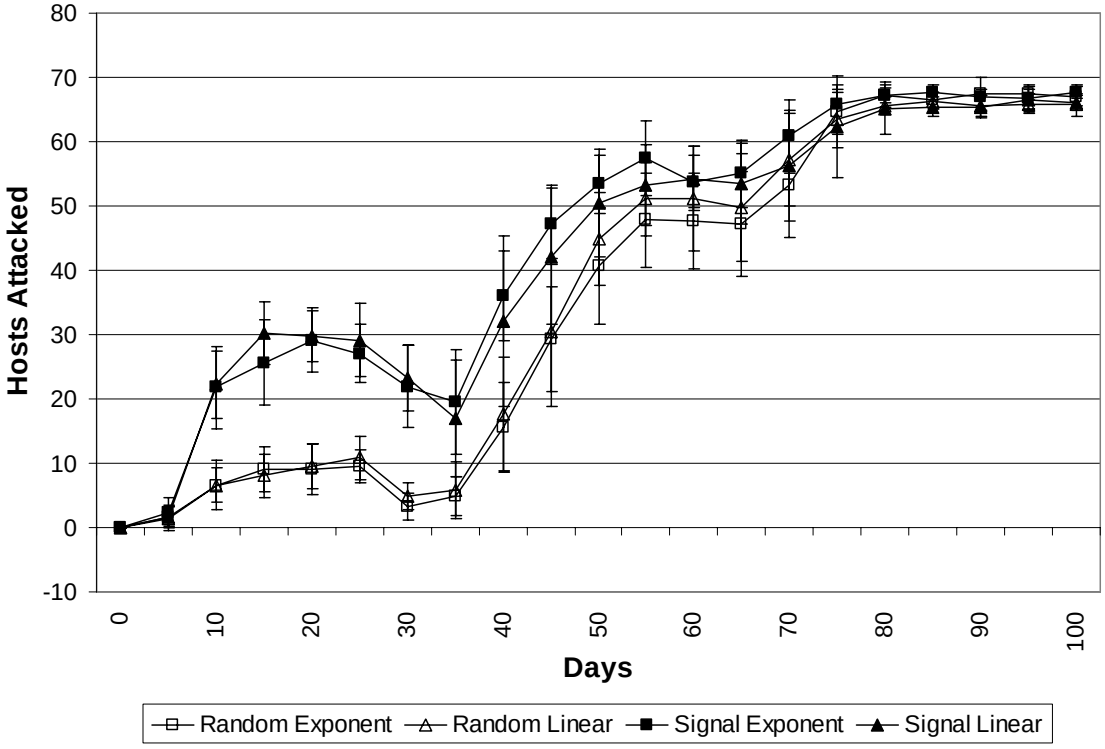

Hosts Attacked
80
70
60
50
40
30
20
10
0
-10
0
10
20
30
40
50
60
70
80
90
100
Days
Random Exponent
Random Linear
Signal Exponent
Signal Linear

Table 8. Difference in number of hosts attacked for parasitoids following signals and parasitoids randomly foraging. Negative numbers indicate that randomly foraging parasitoids had a higher mean number of hosts attacked than parasitoids following signals. The columns are as follows: “Induction” is the induction delay in days, “Relaxation” is the relaxation delay in days, “Density” is the herbivore host density, “Host” is the oldest viable instar host, “Distance” refers to the distance bias of the parasitoid, and “Pattern” is which pattern the parameter combinations were classified as. In the Distance column, “Exp” refers to an exponential bias, and “Lin” refers to a linear bias. In the Pattern column, the parameter combinations that are seen in the time series in Figure 4 are marked by an asterisk. Numbers in bold indicate that the means are significantly different at a $p < 0.05$ level. To aid in interpretation, the following shading pattern was employed.

-0.1 to 0.1	
-0.2 to -0.9	0.2 to 0.9
-1.0 to -2.5	1.0 to 2.5
-2.6 to -5.0	2.6 to 5.0
-5.1+	5.1+

Table 8. Differences in Mean Hosts Attacked Between Parasitoids Following Signals and Randomly Foraging																									
					Day																				
Induction	Relaxation	Density	Host	Distance	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100	Pattern
1	1	Low	1	Exp	-0.1	6.4	5.0	4.9	5.6	0.0	0.1	3.2	4.2	4.1	3.6	1.2	1.0	4.0	3.5	1.8	0.3	-2.9	-4.5	-8.7	D
1	1	Low	1	Lin	0.8	6.3	4.8	5.2	4.6	0.0	1.2	3.0	4.4	6.4	8.8	5.0	3.8	5.8	6.2	5.4	1.8	4.8	7.9	3.8	
3	1	Low	1	Exp	0.5	-1.6	-1.2	-1.0	-1.2	0.0	-0.8	-1.3	-0.8	-0.9	-1.4	0.4	-2.5	-0.6	0.0	1.3	0.0	2.5	0.5	2.7	A
3	1	Low	1	Lin	0.0	-1.4	-1.2	-1.1	-1.4	0.0	-0.5	-1.8	-1.8	-2.4	-4.4	-1.7	-1.6	-1.7	-4.3	-5.4	-5.1	-6.5	-5.6	-6.9	
5	1	Low	1	Exp	0.3	0.0	-1.8	-1.8	-1.2	0.0	-0.2	-0.8	-0.7	-1.5	-1.0	-0.2	0.7	0.4	-1.9	-2.0	0.5	5.9	4.3	4.2	B
5	1	Low	1	Lin	0.0	-0.5	-1.1	-1.4	-1.3	0.0	0.9	-2.0	-2.2	-2.8	-1.7	-0.9	0.1	-3.4	-2.9	-2.2	-2.8	-1.2	-1.5	-1.8	
1	3	Low	1	Exp	0.0	5.4	3.7	3.4	4.1	0.0	1.8	8.7	7.2	7.0	5.2	3.9	3.5	4.7	7.4	7.4	12	11	9.4	6.0	D
1	3	Low	1	Lin	0.6	4.9	5.2	4.1	4.0	0.0	4.2	5.8	6.7	6.0	2.4	1.8	1.2	3.1	5.2	4.8	4.3	-1.6	0.3	0.9	
3	3	Low	1	Exp	0.0	-1.9	-2.0	-0.7	-0.8	0.0	-0.4	-1.7	-0.8	-1.2	-2.2	-1.9	-1.8	-2.7	-4.1	-2.9	-4.3	-5.0	-2.6	-3.8	A*
3	3	Low	1	Lin	-0.1	-2.0	-1.5	-0.7	0.3	0.0	-0.9	-1.7	-2.8	-2.8	-1.8	-0.6	-1.1	-2.3	-2.7	-3.0	-4.8	-0.8	-4.9	-4.6	
5	3	Low	1	Exp	-0.1	-0.9	-0.9	-0.9	-0.7	0.0	-0.4	-3.2	-1.8	-3.4	-3.0	0.0	-0.5	-1.1	-4.3	-5.8	-2.6	-1.7	-2.5	2.4	A
5	3	Low	1	Lin	-0.1	-1.2	-1.2	-0.7	-0.9	0.0	-0.1	-1.1	-0.7	-1.5	-0.5	-1.2	0.3	0.3	0.0	-2.2	-1.1	3.3	1.7	5.0	
1	5	Low	1	Exp	-0.6	4.9	3.2	3.9	3.2	0.0	0.5	3.7	5.3	4.7	5.0	3.6	2.7	4.8	2.9	3.0	6.1	4.4	2.7	3.2	D
1	5	Low	1	Lin	-0.1	6.2	4.6	3.4	3.2	0.0	2.4	6.0	7.4	7.4	5.2	4.0	2.9	3.8	5.5	7.9	4.8	1.3	4.5	2.6	
3	5	Low	1	Exp	0.6	-1.6	-0.8	-1.6	-0.6	0.0	-0.5	-2.1	-1.9	-1.7	-0.8	-1.4	-2.4	-1.4	-3.4	-0.7	-2.3	-3.3	0.1	-0.4	A
3	5	Low	1	Lin	0.1	-1.5	-1.2	-0.4	-0.3	0.0	0.1	-1.3	-2.1	-2.8	-1.7	-2.2	-1.4	-1.7	-1.9	-3.9	-3.5	-4.9	-4.2	-4.7	
5	5	Low	1	Exp	0.9	-0.8	-1.5	-1.5	-0.3	0.0	-0.8	-1.9	-3.4	-4.9	-4.2	-3.3	-3.1	-0.9	-6.5	-6.4	-11	-10	-9.0	-8.5	A
5	5	Low	1	Lin	0.4	-0.5	-1.3	-0.7	-0.9	0.0	-0.1	-0.8	-1.3	-1.8	-2.1	-1.0	-1.3	1.3	-0.2	2.5	0.1	2.6	0.1	3.0	
1	1	High	1	Exp	-0.5	8.0	6.0	3.7	5.8	0.0	5.4	12	8.9	5.2	3.9	0.7	3.3	2.1	1.6	-0.8	1.8	1.2	-1.2	-0.8	D
1	1	High	1	Lin	-0.5	9.0	6.6	6.0	6.4	0.0	7.2	12	7.2	3.2	0.4	-2.5	-0.1	4.6	2.7	1.7	-1.1	1.3	3.2	1.5	
3	1	High	1	Exp	0.3	-2.0	-2.1	-2.4	-1.8	0.0	-2.6	-5.6	-6.5	-4.3	-2.1	-3.2	-5.5	-5.3	-1.7	1.4	1.1	0.8	1.0	-1.6	B
3	1	High	1	Lin	-0.4	-2.4	-1.1	-1.0	-1.4	0.0	-1.4	-3.3	-4.7	-0.7	0.8	-0.7	-0.6	-1.7	-0.8	2.7	0.9	-1.1	1.5	2.9	
5	1	High	1	Exp	1.4	-3.3	-2.2	-1.2	-1.7	0.0	-2.4	-6.5	-2.3	-0.7	-4.0	-1.2	-1.0	-1.0	0.6	0.1	-0.1	0.2	-0.8	-2.9	B
5	1	High	1	Lin	-0.3	-3.1	-2.8	-1.8	-0.9	0.0	-1.1	-6.9	3.0	3.1	2.5	1.7	1.9	7.7	8.9	-0.8	-1.5	0.0	1.0	-0.8	
1	3	High	1	Exp	0.8	8.7	4.4	4.7	3.0	0.0	3.3	8.4	3.8	0.9	-2.8	-0.3	-3.8	-4.2	-0.5	0.8	0.6	0.8	1.0	0.9	D
1	3	High	1	Lin	0.6	8.9	6.4	5.2	5.7	0.0	5.4	10	6.8	-0.1	0.0	-0.4	1.8	2.8	-1.2	0.8	0.4	2.0	-0.1	0.3	

Table 8. Differences in Mean Hosts Attacked Between Parasitoids Following Signals and Randomly Foraging (continued)

					Day																			
Induction	Relaxation	Density	Host	Distance	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100	Pattern
3	3	High	1	Exp	0.0	-1.9	-1.6	-1.0	-2	0.0	-2.8	-4.7	0.2	3.4	1.5	6.4	-0.6	1.3	-2.0	-1.4	-0.3	4.5	-0.5	-1.4	B
3	3	High	1	Lin	-0.4	-2.1	-2.2	-0.2	-1.7	0.0	-4.0	-6.9	-2.6	-2.5	-1.6	1.2	-2.6	-1.6	-1.4	1.6	1.3	-1.4	2.5	0.1	
5	3	High	1	Exp	-0.1	-2.1	-2.3	-0.2	-1.5	0.0	-2.9	-6.4	-0.7	0.3	-3.4	1.9	-1.4	-3.3	-2.5	4.1	-0.3	2.4	-0.8	-0.9	B
5	3	High	1	Lin	0.3	-2.2	-1.3	-0.8	-1.3	0.0	-1.7	-5.3	-3.0	-0.6	-3.4	-3.4	-0.5	0.9	-0.5	-1.3	0.1	0.1	1.4	-0.5	
1	5	High	1	Exp	-1.0	7.8	3.2	3.7	3.9	0.0	4.5	6.1	1.8	1.1	1.4	4.1	-2.4	-2.7	-0.9	-0.3	-2.5	-1.0	-2.9	1.2	D
1	5	High	1	Lin	0.7	9.5	6.8	4.2	3.8	0.0	6.3	11	8.2	6.4	5.0	2.5	2.5	4.2	0.6	-1.5	2.6	-0.5	-0.8	2.3	
3	5	High	1	Exp	0.2	-1.4	0.0	-2.2	-0.8	0.0	-1.1	-2.4	-2.3	-2.3	-0.7	0.3	-3.8	-2.1	-5.3	3.0	0.6	-0.8	0.3	1.5	B
3	5	High	1	Lin	0.3	-3.4	-2.3	-1.4	-1.3	0.0	-1.7	0.3	1.6	-2.7	1.4	1.5	0.2	5.7	4.0	-2.1	1.7	2.8	2.7	-0.9	
5	5	High	1	Exp	-0.6	-2.2	-2.4	-0.7	-0.8	0.0	-2.9	-9.9	-8.3	-4.0	0.9	3.6	-0.8	-8.1	-4.1	-0.4	2.4	1.8	-1.5	-0.5	B*
5	5	High	1	Lin	0.4	-3.1	-2.1	-0.9	-1.9	0.0	-1.2	-2.8	-1.1	0.6	-1.5	0.9	6.9	3.3	1.3	-1.7	0.5	1.2	0.1	0.2	
1	1	Low	2	Exp	-0.1	0.2	0.6	-0.5	-0.9	0.3	-0.5	-0.2	-1.2	-1.8	-2.7	-3.1	-1.0	-1.2	-2.8	-3.2	-5.1	-5.6	-4.3	-7.1	C*
1	1	Low	2	Lin	0.2	12	9.9	10	10	2.0	2.3	7.4	12	15	11	8.9	7.6	13	12	14	9.7	3.5	3.7	2.4	
3	1	Low	2	Exp	-0.3	-0.2	0.5	-0.4	0.4	0.0	-0.5	-1.3	1.4	1.1	0.5	1.6	0.0	-2.2	-2.1	0.7	2.5	5.6	1.8	-0.3	C
3	1	Low	2	Lin	-0.6	6.2	5.6	4.9	7.2	2.0	-0.5	1.2	8.7	10	12	9.5	8.0	4.6	7.4	9.7	9.8	12	11	11	
5	1	Low	2	Exp	0.4	1.0	-1.0	1.0	-0.2	-0.4	-0.1	1.1	1.1	1.5	0.4	1.4	1.5	0.9	-1.5	1.6	2.9	2.1	2.0	-0.1	B
5	1	Low	2	Lin	-0.4	3.1	-0.3	0.8	0.7	2.6	-0.5	0.4	2.3	3.3	4.5	3.3	1.5	2.4	4.4	4.4	8.4	11	6.4	9.7	
1	3	Low	2	Exp	0.4	-0.5	-0.8	-1.2	-0.5	-0.2	0.2	1.2	2.1	1.7	4.1	2.6	2.5	5.8	4.8	8.5	11	12	13	12	C
1	3	Low	2	Lin	0.2	10	9.9	9.2	9.1	2.0	0.8	7.4	13	13	9.2	11	3.9	7.6	12	15	11	11	7.1	5.4	
3	3	Low	2	Exp	0.2	0.8	0.1	0.8	0.2	-0.4	0.9	1.0	0.4	-0.4	1.3	-0.4	0.7	3.1	0.1	1.6	-0.2	-2.9	-0.1	0.9	C
3	3	Low	2	Lin	-0.4	5.6	5.7	5.2	4.3	1.6	-0.5	1.9	3.3	1.6	4.5	2.5	1.4	1.9	-1.7	-4.6	-3.9	-5.4	-3.1	-2.9	
5	3	Low	2	Exp	-0.1	-1.7	0.5	-0.7	-1.1	-0.1	0.8	0.9	-0.6	-0.5	-2.1	-2.4	-1.5	-1.9	0.0	-0.1	-1.3	0.1	-1.8	-6.3	A
5	3	Low	2	Lin	0.2	2.2	0.0	-0.9	0.6	1.2	-0.7	-1.1	-0.7	-3.4	-1.8	-2.7	-2.4	-0.7	-2.2	-5.1	-10	-9.4	-9.0	-12	
1	5	Low	2	Exp	-0.7	0.4	-0.3	-0.7	0.1	0.0	-0.3	0.4	0.0	-0.2	2.3	4.1	0.8	1.5	3.1	6.8	4.7	4.0	3.8	6.2	C
1	5	Low	2	Lin	0.0	9.7	9.7	5.0	7.9	2.0	2.4	6.3	8.9	7.8	11	9.1	8.2	9.2	6.0	2.8	8.9	2.6	3.9	6.0	
3	5	Low	2	Exp	0.0	4.3	4.4	3.1	4.1	1.6	-1.2	0.9	5.7	5.5	7.2	6.2	3.6	1.2	3.6	7.4	6.5	6.2	4.1	4.4	D
3	5	Low	2	Lin	0.1	4.6	6.1	4.0	3.7	2.0	-1.2	3.1	6.5	5.2	8.4	3.6	2.1	2.6	4.1	5.5	3.9	5.0	-1.3	2.4	

Table 8. Differences in Mean Hosts Attacked Between Parasitoids Following Signals and Randomly Foraging (continued)																									
					Day																				
Induction	Relaxation	Density	Host	Distance	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100	Pattern
5	5	Low	2	Exp	0.0	2.3	-1.3	-2.4	0.1	1.7	0.1	-0.8	-0.8	0.1	0.4	-1.1	1.5	1.1	-1.5	-1.6	1.6	-1.4	-2.0	-0.2	B
5	5	Low	2	Lin	-0.1	1.2	0.5	-0.6	-0.1	1.2	-0.9	0.8	2.5	4.2	3.5	2.0	1.4	2.8	6.0	11	12	11	7.7	8.8	
1	1	High	2	Exp	-0.5	16	10	10	8.8	2.2	3.9	9.7	7.7	4.8	0.0	3.8	2.4	-5.3	0.8	4.3	-0.1	1.4	-0.3	-0.4	D
1	1	High	2	Lin	0.1	19	14	14	13	2.3	4.5	13	11	5.8	0.6	1.2	0.1	-1.9	1.7	0.5	-0.9	-0.6	1.6	0.6	
3	1	High	2	Exp	0.4	12	5.5	3.4	6.2	2.5	-2.1	11	5.3	2.9	4.4	1.1	3.7	0.9	1.0	0.5	0.3	1.3	0.3	0.4	D
3	1	High	2	Lin	-0.1	11	7.8	8.5	5.1	2.9	-1.5	9.7	4.9	6.5	3.7	1.6	1.0	2.1	0.4	2.5	0.5	-0.8	0.4	-0.3	
5	1	High	2	Exp	-0.2	1.8	0.7	-0.9	1.9	1.4	-3.6	-4.6	-2.8	-1.2	1.8	-3.7	1.5	-6.6	-1.1	0.5	2.0	-0.1	0.8	-0.4	B
5	1	High	2	Lin	-0.2	3.3	0.4	-0.3	1.2	1.9	-4.8	-9.7	-3.8	-6.3	-3.5	-0.4	-2.7	-10	-3.1	1.6	-0.4	1.7	1.1	-0.5	
1	3	High	2	Exp	-0.2	14	12	9.4	9.5	3.2	2.4	15	8.8	0.1	0.0	1.3	-0.1	0.4	0.4	-0.7	1.9	0.3	-0.3	-0.5	D
1	3	High	2	Lin	-0.1	18	12	9.5	11	1.6	4.3	11	10	2.7	2.3	2.6	-1.5	-1.0	-0.5	1.4	0.1	0.2	1.1	-0.2	
3	3	High	2	Exp	0.6	7.5	6.0	5.5	5.1	2.7	-1.8	5.9	9.9	5.5	2.4	5.7	-0.2	3.8	-0.3	-1.3	1.5	1.0	0.3	1.1	D
3	3	High	2	Lin	0.7	10	8.7	4.8	4.5	1.9	-3.0	12	5.6	3.0	3.1	3.1	-1.6	-1.2	-0.5	-0.5	1.5	-1.5	1.8	-0.4	
5	3	High	2	Exp	-0.5	1.3	0.2	0.2	0.2	2.8	-3.3	-6.6	-2.8	-1.9	-1.3	0.7	-0.7	0.0	0.5	0.2	-0.3	-1.1	-0.8	1.4	B
5	3	High	2	Lin	0.1	1.6	1.3	0.9	0.8	2.7	-1.6	-1.3	1.4	3.8	1.4	0.0	1.3	3.8	4.9	0.3	1.1	-1.6	-0.3	0.3	
1	5	High	2	Exp	0.5	12	9.6	9.1	7.3	1.4	5.6	11	6.9	6.0	6.2	4.5	1.3	-3.2	0.3	0.2	-0.4	-0.2	-0.5	0.8	D
1	5	High	2	Lin	0.3	16	9.1	9.1	7.8	2.6	6.1	15	8.4	4.3	1.7	3.6	5.1	0.8	-1.8	1.2	-1.3	0.9	-2.1	0.6	
3	5	High	2	Exp	0.0	8.9	4.9	1.9	4.5	1.8	-1.5	0.4	0.6	2.7	1.4	1.9	1.8	-2.5	-4.6	-0.8	1.6	-1.5	1.2	-0.1	D
3	5	High	2	Lin	0.5	9.7	9.4	5.1	4.9	3.2	-0.7	9.0	8.3	6.6	3.5	0.1	5.1	3.7	4.7	-0.1	1.6	-0.1	0.2	0.5	
5	5	High	2	Exp	-0.4	2.8	-0.5	-0.7	-0.7	2.8	-1.5	-2.4	-2.1	-0.5	-2.4	-0.6	-0.3	3.1	1.6	-0.5	0.0	0.3	0.6	0.1	B
5	5	High	2	Lin	-0.1	3.3	0.3	0.5	0.3	2.2	-2.3	-0.4	5.8	3.3	4.3	-0.5	-0.8	6.3	2.7	-0.3	-1.1	-0.3	-0.5	-2.6	
1	1	Low	5	Exp	0.1	10	12	14	12	8.2	5.7	10	12	15	16	16	17	16	16	12	11	11	8.4	6.5	D
1	1	Low	5	Lin	-0.6	11	16	15	16	11	5.8	9.5	13	13	15	18	16	13	8.8	5.3	3.4	3.3	-2.0	-2.8	
3	1	Low	5	Exp	0.0	3.5	9.5	12	11	11	3.0	3.1	8.8	17	15	16	15	13	12	14	11	13	6.6	8.9	D
3	1	Low	5	Lin	0.3	4.9	9.2	15	15	12	5.2	3.1	8.5	14	18	16	13	13	10	8.5	7.8	9.1	7.8	8.6	
5	1	Low	5	Exp	0.7	0.9	7.2	9.8	8.8	11	3.1	-0.7	2.1	12	18	22	20	16	13	14	16	19	17	19	D
5	1	Low	5	Lin	0.2	2.6	9.9	10	10	12	3.7	0.6	8.2	9.6	12	13	11	11	7.2	9.7	7.4	6.1	7.8	6.2	
1	3	Low	5	Exp	0.6	11	14	15	14	8.1	4.6	1.6	7.4	11	12	12	11	10	7.6	4.2	-0.6	-2.1	-3.9	-4.8	D
1	3	Low	5	Lin	-0.2	11	15	18	16	12	6.4	8.2	14	18	18	16	15	12	15	14	13	10	6.9	5.5	
3	3	Low	5	Exp	-0.1	4.3	12	9.8	10	9.9	4.1	3.7	9.7	12	16	14	13	12	13	8.8	9.1	7.8	9.7	9.0	D
3	3	Low	5	Lin	0.3	5.8	12	13	14	11	3.2	6.6	13	17	13	16	14	11	12	12	12	9.4	4.2	6.1	

Table 8. Differences in Mean Hosts Attacked Between Parasitoids Following Signals and Randomly Foraging (continued)

					Day																		
Induction	Relaxation	Density	Host	Distance	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100	Pattern
5	3	Low	5	Exp	0.8	1.5	5.6	7.4	9.4	9.7	3.4	-0.1	4.6	7.2	14	11	13	11	9.2	8.4	9.1	9.2	8.6	7.4	D
5	3	Low	5	Lin	-0.2	1.2	7.9	12	9.4	11	4.1	-0.1	5.1	5.3	4.8	11	11	8.5	9.2	4.4	0.5	3.1	3.4	2.2	
1	5	Low	5	Exp	-0.3	9.4	12	13	11	8.3	4.0	6.3	13	13	13	14	13	12	11	12	14	10	5.8	7.5	D
1	5	Low	5	Lin	-0.1	12	14	14	14	11	6.2	6.3	11	15	11	9.0	9.4	7.6	8.8	6.8	-0.1	-4.0	-8.2	-5.1	
3	5	Low	5	Exp	-0.1	6.9	12	9.6	8.4	8.7	3.0	2.6	6.9	7.8	11	11	8.9	7.6	9.4	9.9	9.1	4.6	4.5	3.7	D
3	5	Low	5	Lin	0.1	3.9	7.3	10	10	11	4.4	2.8	6.5	10	10	13	11	11	10	9.3	6.9	6.2	7.3	6.7	
5	5	Low	5	Exp	-0.2	1.5	6.2	5.4	7.7	9.0	3.3	0.4	3.2	8.9	9.0	11	10	10	8.5	7.4	7.2	4.6	4.8	3.0	D
5	5	Low	5	Lin	-0.1	1.2	9.0	8.3	8.9	10	4.5	0.6	5.7	8.7	9.8	11	9.8	4.8	5.2	5.1	3.9	2.5	3.0	2.0	
1	1	High	5	Exp	0.6	15	17	20	18	19	15	21	18	13	9.6	6.2	7.8	7.5	1.1	0.0	1.3	-0.6	-0.8	0.7	D*
1	1	High	5	Lin	0.3	16	22	20	18	19	11	14	12	5.6	2.1	3.2	3.6	-1.0	-1.1	-0.3	-0.9	-0.1	0.7	0.3	
3	1	High	5	Exp	0.5	8.8	14	16	15	16	6.6	12	14	9.0	6.9	6.0	8.2	6.2	2.8	0.5	-0.2	0.5	0.5	0.5	D
3	1	High	5	Lin	-1.1	6.7	16	19	18	18	6.5	14	13	11	8.3	8.1	7.4	2.5	1.1	-0.2	0.0	-0.5	0.0	0.7	
5	1	High	5	Exp	0.0	1.9	11	9.4	11	15	6.7	2.2	10	4.4	3.3	3.7	6.2	1.5	0.9	1.2	0.5	0.7	-0.2	0.6	D
5	1	High	5	Lin	-0.4	1.8	11	15	15	20	4.0	-4.5	2.6	3.6	2.8	7.9	4.2	-2.0	-3.6	0.0	-0.2	0.1	0.3	-0.3	
1	3	High	5	Exp	-0.9	13	14	18	14	12	10	11	15	7.1	1.7	1.8	4.5	1.1	1.6	-0.2	0.5	-0.9	0.0	0.5	D
1	3	High	5	Lin	0.5	15	18	19	20	13	7.5	13	16	8.9	5.3	4.1	2.4	3.3	1.8	0.5	0.7	0.1	0.3	-0.5	
3	3	High	5	Exp	0.3	10	15	12	14	14	4.7	5.9	8.7	2.5	5.2	1.7	3.1	0.6	-3.4	-0.8	0.5	0.0	-0.3	-1.0	D
3	3	High	5	Lin	-0.4	11	15	17	15	15	6.7	16	16	12	6.9	5.3	4.8	5.2	3.7	0.4	-0.5	0.8	0.6	0.4	
5	3	High	5	Exp	0.1	2.0	9.3	10	11	13	2.0	-3.2	7.8	3.6	-0.1	2.7	1.5	-1.3	0.7	-0.1	-0.8	-0.1	-0.1	-0.2	D
5	3	High	5	Lin	-0.6	2.5	11	13	15	16	4.0	1.6	5.5	4.4	3.1	0.9	0.9	1.0	-0.7	-0.5	-0.1	-0.1	-0.5	0.3	
1	5	High	5	Exp	-0.1	12	15	15	11	9.1	6.7	14	8.5	3.6	1.9	1.3	3.7	3.3	1.1	-0.7	-1.3	0.6	-0.6	-0.2	D
1	5	High	5	Lin	0.2	15	16	14	14	12	12	13	7.1	3.4	1.7	0.8	-0.8	0.1	1.1	-0.2	0.3	-0.8	0.1	0.5	
3	5	High	5	Exp	-1.2	6.0	11	12	13	11	4.3	4.8	9.8	6.1	1.2	2.1	4.5	1.5	-0.1	0.8	0.3	-0.5	0.0	0.0	D
3	5	High	5	Lin	0.6	7.8	13	16	13	13	1.7	6.1	8.0	3.0	3.4	-0.9	1.0	-3.0	-2.5	-1.2	0.6	0.4	0.3	0.0	
5	5	High	5	Exp	0.4	1.0	13	12	11	13	4.6	0.4	5.2	6.6	3.5	3.7	2.5	4.3	3.6	1.0	-0.7	-0.7	-0.5	0.0	D
5	5	High	5	Lin	0.0	2.5	10	13	9.9	14	5.6	1.9	5.8	3.1	5.4	3.7	2.7	-0.6	-0.7	0.0	0.5	0.0	0.1	0.1	

Table 9. Relative advantage of for parasitoids following signals, as calculated by the difference in number of attacked for hosts following signals and parasitoids randomly foraging divided by the number of attacked for hosts randomly foraging. Negative numbers indicate that randomly foraging parasitoids had a higher relative advantage than parasitoids following signals. The columns are as follows: "Induction" is the induction delay in days, "Relaxation" is the relaxation delay in days, "Density" is the herbivore host density, "Host" is the oldest viable instar host, "Distance" refers to the distance bias of the parasitoid, and "Pattern" is which pattern the parameter combinations were classified as. In the Distance column, "Exp" refers to an exponential bias, and "Lin" refers to a linear bias. To aid in interpretation, the following shading pattern was employed.

-0.1 to 0.1	
-0.2 to -0.5	0.2 to 0.5
-0.6 to -1.0	0.6 to 1.0
-1.1 to -2.0	1.1 to 2.0
-2.1+	2.1+

Table 9. Relative Advantage for Parasitoids Following Signals																									
					Day																				
Induction	Relaxation	Density	Host	Distance	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100	Pattern
1	1	Low	1	Exp	0.8	2.8	1.6	1.7	1.2	0.0	1.3	1.1	1.6	0.3	0.1	-0.1	0.5	0.3	0.8	0.2	-0.1	-0.4	0.0	0.0	D
1	1	Low	1	Lin	1.7	3.6	2.5	3.2	2.8	0.0	1.3	0.9	1.1	1.2	1.3	0.9	1.2	1.2	0.8	0.4	0.1	0.2	0.4	0.2	
3	1	Low	1	Exp	-0.4	-0.6	-0.5	-0.4	-0.5	0.0	-0.3	-0.7	-0.5	-0.6	-0.6	-0.5	0.0	-0.1	-0.3	-0.2	-0.2	-0.2	-0.2	-0.2	A
3	1	Low	1	Lin	0.0	-0.7	-0.7	-0.6	-0.6	0.0	-0.7	-0.8	-0.5	-0.4	-0.5	-0.3	-0.4	-0.4	-0.5	-0.3	-0.2	-0.2	-0.2	-0.3	
5	1	Low	1	Exp	0.0	0.0	-0.5	-0.5	-0.2	0.0	1.2	-0.4	-0.6	-0.6	-0.1	-0.1	0.2	-0.7	-0.2	0.1	-0.1	0.0	0.0	0.0	B
5	1	Low	1	Lin	0.0	-0.2	-0.6	-0.6	-0.6	0.0	3.4	-0.6	-0.5	-0.4	-0.3	-0.2	0.0	-0.5	-0.3	-0.1	-0.1	0.0	-0.1	-0.1	
1	3	Low	1	Exp	0.3	1.8	0.8	1.1	1.7	0.0	4.7	1.3	0.8	0.3	-0.4	0.2	0.1	0.3	0.0	0.0	0.0	-0.1	0.0	-0.1	D
1	3	Low	1	Lin	1.5	2.3	2.9	1.5	2.1	0.0	5.5	2.4	1.5	0.9	0.3	0.3	0.2	0.5	0.5	0.3	0.2	-0.1	0.0	0.0	
3	3	Low	1	Exp	-0.3	-0.8	-0.8	-0.6	0.1	0.0	-1.1	-0.5	-0.3	-0.2	0.0	0.0	-0.3	-0.5	-0.1	0.0	0.0	-0.1	0.0	-0.1	A
3	3	Low	1	Lin	-0.1	-0.8	-0.6	-0.4	0.2	0.0	-0.9	-0.7	-0.6	-0.4	-0.2	-0.1	-0.3	-0.4	-0.3	-0.2	-0.2	0.0	-0.2	-0.2	
5	3	Low	1	Exp	-0.1	-0.4	-0.3	-0.3	0.1	0.0	-0.3	0.0	-0.1	-0.2	0.2	-0.2	0.0	-0.4	0.3	0.3	0.0	-0.2	-0.1	0.0	A
5	3	Low	1	Lin	-0.1	-0.5	-0.5	-0.3	-0.4	0.0	-0.3	-0.5	-0.2	-0.2	-0.1	-0.2	0.1	0.1	0.0	-0.1	0.0	0.1	0.1	0.2	
1	5	Low	1	Exp	0.1	0.8	0.8	0.9	1.2	0.0	3.2	1.4	1.2	0.6	0.6	0.3	0.6	0.7	0.3	0.1	-0.3	-0.2	0.0	0.2	D
1	5	Low	1	Lin	-0.1	2.9	1.8	1.4	1.2	0.0	5.9	3.3	2.1	1.9	0.9	0.9	0.7	0.7	0.7	0.6	0.3	0.1	0.2	0.1	
3	5	Low	1	Exp	-0.2	-0.5	-0.3	-0.1	-0.1	0.0	0.2	-0.2	-0.2	-0.3	-0.3	-0.4	-0.3	-0.3	-0.3	-0.2	-0.1	0.1	-0.3	-0.2	A
3	5	Low	1	Lin	0.1	-0.7	-0.6	-0.2	-0.2	0.0	0.4	-0.6	-0.5	-0.4	-0.2	-0.3	-0.3	-0.3	-0.2	-0.2	-0.1	-0.2	-0.2	-0.2	
5	5	Low	1	Exp	0.6	-0.1	-0.4	-0.2	-0.1	0.0	-0.3	-0.3	-0.4	0.0	0.2	-0.2	-0.3	0.3	-0.1	0.2	-0.2	-0.1	-0.1	-0.2	A
5	5	Low	1	Lin	0.7	-0.2	-0.6	-0.4	-0.5	0.0	-0.1	-0.4	-0.3	-0.3	-0.3	-0.2	-0.3	0.2	0.0	0.2	0.0	0.1	0.0	0.1	
1	1	High	1	Exp	-0.5	0.6	0.3	0.6	0.8	0.0	1.6	0.1	-0.1	-0.1	-0.7	-0.4	0.0	-0.1	-0.2	-0.2	-0.1	0.0	-0.1	0.0	D
1	1	High	1	Lin	-0.3	2.1	1.4	1.5	1.4	0.0	1.7	0.9	0.3	0.1	0.0	-0.1	0.0	0.1	0.1	0.0	0.0	0.0	0.1	0.0	
3	1	High	1	Exp	-0.1	-0.1	0.1	0.0	-0.6	0.0	-0.1	0.0	0.1	0.0	0.0	0.6	0.0	0.4	-0.6	-0.3	-0.2	0.0	0.0	0.1	B
3	1	High	1	Lin	-0.2	-0.6	-0.3	-0.3	-0.3	0.0	-0.4	-0.2	-0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.1	
5	1	High	1	Exp	-0.2	-0.1	-0.2	0.0	-0.1	0.0	-0.2	-0.3	0.0	0.0	0.2	0.5	0.4	-0.2	-0.2	-0.3	0.2	-0.1	0.0	-0.1	B
5	1	High	1	Lin	-0.1	-0.7	-0.6	-0.4	-0.2	0.0	-0.5	-0.5	0.2	0.1	0.1	0.1	0.1	0.2	0.2	0.0	0.0	0.0	0.0	0.0	
1	3	High	1	Exp	0.1	1.1	0.3	0.7	0.1	0.0	1.4	-0.1	0.1	-0.1	-0.3	-0.3	0.1	-0.1	0.1	-1.0	0.0	-0.2	0.3	-0.3	D
1	3	High	1	Lin	0.4	2.0	1.8	1.2	1.5	0.0	1.7	0.7	0.3	0.0	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	

Table 9. Relative Advantage for Parasitoids Following Signals (continued)																								
					Day																			
Ind.	Relaxation	Density	Host	Distance	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100	Pattern
3	3	High	1	Exp	-0.5	-0.8	-0.2	-0.2	-0.2	0.0	-1.0	-0.2	0.0	0.2	0.4	0.2	-0.2	0.2	0.4	-0.4	-0.1	-0.1	-0.1	-0.4	B
3	3	High	1	Lin	-0.2	-0.6	-0.5	-0.1	-0.4	0.0	-0.8	-0.5	-0.1	-0.1	-0.1	0.0	-0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
5	3	High	1	Exp	0.2	-0.4	-0.3	0.2	0.0	0.0	-0.3	0.0	0.1	0.0	-0.2	0.0	-0.3	0.1	0.0	0.0	0.1	0.1	0.1	0.0	B
5	3	High	1	Lin	0.2	-0.5	-0.3	-0.2	-0.4	0.0	-0.4	-0.4	-0.1	0.0	-0.1	-0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
1	5	High	1	Exp	0.0	0.0	0.4	0.4	1.0	0.0	0.7	0.1	0.2	-0.3	-0.4	0.1	0.0	-0.2	-0.5	0.3	-0.2	0.1	0.5	-0.1	D
1	5	High	1	Lin	0.4	2.2	1.8	1.1	1.0	0.0	1.8	1.0	0.4	0.2	0.2	0.1	0.1	0.1	0.0	0.0	0.1	0.0	0.0	0.0	
3	5	High	1	Exp	0.2	-1.8	-0.9	-0.6	-0.4	0.0	-0.4	0.1	0.2	-0.4	0.2	0.2	0.0	0.5	0.4	-0.4	0.3	0.6	0.5	-0.1	B
3	5	High	1	Lin	0.1	-0.7	-0.6	-0.3	-0.3	0.0	-0.4	0.0	0.1	-0.1	0.0	0.1	0.0	0.1	0.1	0.0	0.0	0.1	0.1	0.0	
5	5	High	1	Exp	0.2	-1.5	-0.8	-0.3	-0.6	0.0	-0.3	-0.4	-0.2	0.1	-0.2	0.2	0.9	0.2	0.2	-0.3	0.1	0.2	0.0	0.0	B
5	5	High	1	Lin	0.2	-0.8	-0.5	-0.2	-0.4	0.0	-0.3	-0.2	-0.1	0.0	0.0	0.0	0.3	0.1	0.0	0.0	0.0	0.0	0.0	0.0	
1	1	Low	2	Exp	-0.1	0.1	0.2	-0.1	-0.3	1.0	-0.5	-0.1	-0.2	-0.2	-0.2	-0.3	-0.2	-0.2	-0.3	-0.2	-0.2	-0.2	-0.1	-0.2	C
1	1	Low	2	Lin	0.2	3.2	3.4	4.0	4.7	9.8	4.1	2.4	1.9	1.8	0.9	1.0	1.0	2.2	1.1	0.8	0.3	0.1	0.1	0.1	
3	1	Low	2	Exp	-0.4	-0.1	0.1	-0.1	0.1	0.0	-0.6	-0.3	0.2	0.1	0.0	0.2	0.0	-0.2	-0.1	0.0	0.1	0.2	0.0	0.0	C
3	1	Low	2	Lin	-0.5	1.6	1.9	1.4	2.4	5.0	-0.7	0.4	1.8	1.6	1.4	1.2	1.4	0.7	0.7	0.6	0.4	0.4	0.4	0.4	
5	1	Low	2	Exp	0.5	0.4	-0.3	0.4	0.0	-0.5	-0.1	0.4	0.2	0.2	0.0	0.1	0.2	0.1	-0.1	0.1	0.1	0.1	0.1	0.0	B
5	1	Low	2	Lin	-0.3	1.1	-0.1	0.3	0.3	7.3	-0.6	0.1	0.4	0.4	0.6	0.4	0.2	0.4	0.5	0.2	0.3	0.4	0.2	0.4	
1	3	Low	2	Exp	0.8	-0.1	-0.2	-0.3	-0.1	-0.3	0.3	0.3	0.4	0.2	0.4	0.3	0.4	0.9	0.4	0.5	0.4	0.4	0.4	0.4	C
1	3	Low	2	Lin	0.2	2.5	2.7	3.5	2.6	4.9	1.2	3.0	2.3	1.6	0.9	1.6	0.6	1.2	1.5	1.0	0.4	0.4	0.2	0.2	
3	3	Low	2	Exp	0.4	0.3	0.0	0.3	0.0	-0.6	1.7	0.4	0.1	0.0	0.1	0.0	0.1	0.5	0.0	0.1	0.0	-0.1	0.0	0.0	C
3	3	Low	2	Lin	-0.4	1.6	1.9	1.9	1.2	3.2	-0.6	0.5	0.5	0.1	0.4	0.2	0.1	0.2	-0.1	-0.2	-0.1	-0.1	-0.1	-0.1	
5	3	Low	2	Exp	-0.1	-0.4	0.1	-0.2	-0.3	-0.3	7.5	0.3	-0.1	-0.1	-0.2	-0.3	-0.2	-0.2	0.0	0.0	0.0	0.0	0.0	-0.2	A
5	3	Low	2	Lin	0.1	0.7	0.0	-0.2	0.2	2.2	-0.6	-0.3	-0.1	-0.3	-0.2	-0.2	-0.3	-0.1	-0.2	-0.2	-0.3	-0.2	-0.2	-0.3	
1	5	Low	2	Exp	-0.7	0.1	-0.1	-0.2	0.0	0.0	-0.3	0.1	0.0	0.0	0.2	0.6	0.1	0.2	0.2	0.4	0.2	0.1	0.1	0.2	C
1	5	Low	2	Lin	-0.1	2.8	2.3	1.1	2.9	4.3	3.7	1.6	1.5	0.8	1.1	1.1	1.6	1.6	0.5	0.1	0.3	0.1	0.1	0.2	
3	5	Low	2	Exp	-0.1	1.1	1.4	1.0	1.6	3.9	-0.8	0.3	1.5	0.7	0.9	1.0	0.6	0.2	0.3	0.5	0.3	0.2	0.1	0.2	D
3	5	Low	2	Lin	0.1	1.1	2.1	1.1	1.2	7.8	-1.0	0.7	1.1	0.6	1.0	0.4	0.3	0.3	0.4	0.3	0.1	0.1	0.0	0.1	

Table 9. Relative Advantage for Parasitoids Following Signals (continued)

					Day																			
Induction	Relaxation	Density	Host	Distance	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100	Pattern
5	5	Low	2	Exp	0.0	0.8	-0.3	-0.5	0.0	8.5	0.5	-0.2	-0.1	0.0	0.0	-0.1	0.2	0.1	-0.1	-0.1	0.1	0.0	-0.1	0.0	B
5	5	Low	2	Lin	-0.1	0.3	0.2	-0.2	0.0	1.9	-0.9	0.3	0.5	0.6	0.4	0.2	0.2	0.4	0.6	0.7	0.5	0.4	0.2	0.3	
1	1	High	2	Exp	-0.2	2.7	1.5	1.4	1.5	3.3	0.8	0.5	0.3	0.1	0.0	0.1	0.1	-0.1	0.0	0.1	0.0	0.0	0.0	0.0	D
1	1	High	2	Lin	0.1	3.3	2.0	2.3	1.9	2.3	1.3	0.8	0.4	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
3	1	High	2	Exp	0.4	1.9	0.8	0.5	0.9	3.3	-0.7	0.6	0.2	0.1	0.1	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	D
3	1	High	2	Lin	-0.1	1.7	1.4	1.6	0.7	3.4	-0.5	0.5	0.2	0.2	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
5	1	High	2	Exp	-0.1	0.3	0.1	-0.2	0.3	1.4	-0.7	-0.2	-0.1	0.0	0.0	-0.1	0.0	-0.1	0.0	0.0	0.0	0.0	0.0	0.0	B
5	1	High	2	Lin	-0.1	0.7	0.1	0.0	0.2	1.9	-0.9	-0.5	-0.1	-0.2	-0.1	0.0	-0.1	-0.2	-0.1	0.0	0.0	0.0	0.0	0.0	
1	3	High	2	Exp	-0.1	2.4	2.0	1.8	1.3	4.2	0.5	1.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	D
1	3	High	2	Lin	-0.1	3.7	1.8	1.4	1.9	1.6	0.8	0.5	0.4	0.1	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
3	3	High	2	Exp	0.5	1.2	1.0	0.8	0.8	4.5	-0.6	0.4	0.4	0.2	0.1	0.2	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	D
3	3	High	2	Lin	0.6	1.5	1.4	0.7	0.7	2.5	-0.5	0.6	0.2	0.1	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
5	3	High	2	Exp	-0.2	0.2	0.0	0.0	0.0	3.7	-0.6	-0.4	-0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	B
5	3	High	2	Lin	0.1	0.2	0.2	0.1	0.1	7.7	-0.4	-0.1	0.1	0.1	0.0	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.0	
1	5	High	2	Exp	0.3	2.3	1.8	1.8	1.1	2.8	1.6	0.7	0.2	0.2	0.2	0.1	0.0	-0.1	0.0	0.0	0.0	0.0	0.0	0.0	D
1	5	High	2	Lin	0.2	2.8	1.4	1.3	1.1	2.7	2.0	1.0	0.3	0.1	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
3	5	High	2	Exp	0.0	1.3	0.8	0.3	0.7	1.9	-0.4	0.0	0.0	0.1	0.0	0.0	0.1	0.0	-0.1	0.0	0.0	0.0	0.0	0.0	D
3	5	High	2	Lin	0.4	1.5	2.1	0.8	0.6	4.5	-0.2	0.5	0.3	0.2	0.1	0.0	0.1	0.1	0.1	0.0	0.0	0.0	0.0	0.0	
5	5	High	2	Exp	-0.3	0.5	-0.1	-0.1	-0.1	8.0	-0.3	-0.2	-0.1	0.0	-0.1	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	B
5	5	High	2	Lin	0.0	0.6	0.0	0.1	0.0	3.1	-0.5	0.0	0.2	0.1	0.1	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	
1	1	Low	5	Exp	0.1	2.9	2.4	2.4	1.9	3.4	3.4	3.4	1.9	1.5	1.2	1.3	1.6	1.8	1.3	0.6	0.3	0.3	0.2	0.2	D
1	1	Low	5	Lin	-0.6	2.7	3.7	2.5	3.0	5.3	3.1	2.4	1.5	0.9	0.9	1.1	1.2	0.8	0.4	0.2	0.1	0.1	0.0	-0.1	
3	1	Low	5	Exp	-0.1	1.0	2.3	2.7	1.8	6.2	1.4	0.8	1.3	1.8	1.1	1.3	1.2	0.9	0.8	0.6	0.3	0.3	0.1	0.2	D
3	1	Low	5	Lin	0.7	1.1	1.8	2.8	2.6	4.0	2.9	0.6	0.9	1.0	1.1	1.1	0.9	1.0	0.6	0.3	0.2	0.2	0.2	0.2	
5	1	Low	5	Exp	0.9	0.3	1.8	1.7	1.6	5.8	1.8	-0.2	0.3	1.2	1.7	2.3	2.4	1.7	1.0	0.7	0.5	0.6	0.5	0.5	D
5	1	Low	5	Lin	0.2	0.9	2.3	1.8	2.0	3.8	1.9	0.2	1.0	0.8	0.7	0.9	0.8	0.8	0.4	0.4	0.2	0.1	0.2	0.1	
1	3	Low	5	Exp	0.8	4.2	2.9	2.6	3.1	3.3	4.0	0.3	1.1	0.9	0.8	0.7	0.8	0.9	0.5	0.2	0.0	0.0	-0.1	-0.1	D
1	3	Low	5	Lin	-0.1	2.7	2.6	3.7	3.4	4.4	4.0	2.6	2.5	1.8	1.4	1.3	1.2	1.0	1.1	0.7	0.4	0.3	0.2	0.1	
3	3	Low	5	Exp	-0.1	1.2	2.6	1.7	1.8	3.5	2.5	1.0	1.3	0.9	1.1	1.0	1.2	1.2	0.8	0.3	0.3	0.2	0.2	0.2	D
3	3	Low	5	Lin	0.5	1.2	2.5	1.9	2.7	5.5	1.6	1.9	1.4	1.3	0.7	1.0	1.0	0.7	0.5	0.4	0.3	0.2	0.1	0.1	

Table 9. Relative Advantage for Parasitoids Following Signals (continued)																								
					Day																			
Induction	Relaxation	Density	Host	Distance	5	10	15	20	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100	Pattern
5	3	Low	5	Exp	1.2	0.4	1.1	1.4	2.0	4.3	1.9	0.0	0.7	0.7	1.1	0.8	1.2	0.9	0.6	0.3	0.3	0.2	0.2	0.2	D
5	3	Low	5	Lin	-0.3	0.3	1.8	2.3	1.6	4.4	2.8	0.0	0.7	0.4	0.3	0.7	0.9	0.6	0.6	0.2	0.0	0.1	0.1	0.0	
1	5	Low	5	Exp	-0.3	2.5	2.7	2.2	2.2	3.0	3.0	2.4	2.2	1.3	1.0	1.1	1.2	1.3	0.7	0.6	0.5	0.3	0.1	0.2	D
1	5	Low	5	Lin	-0.1	4.3	2.7	2.7	2.6	5.4	5.1	1.6	1.4	1.2	0.6	0.5	0.7	0.5	0.5	0.2	0.0	-0.1	-0.2	-0.1	
3	5	Low	5	Exp	-0.1	3.0	3.2	1.8	1.5	4.1	1.7	0.8	1.1	0.8	1.0	0.8	0.8	0.7	0.7	0.5	0.3	0.1	0.1	0.1	D
3	5	Low	5	Lin	0.1	1.2	1.5	2.1	1.7	4.0	3.0	0.9	0.9	0.8	0.7	1.0	1.0	1.0	0.7	0.4	0.2	0.2	0.2	0.2	
5	5	Low	5	Exp	-0.2	0.4	1.2	1.0	1.5	4.0	2.2	0.2	0.6	1.0	0.7	0.8	0.9	0.9	0.6	0.4	0.3	0.1	0.1	0.1	D
5	5	Low	5	Lin	-0.1	0.3	1.9	1.5	2.0	5.2	2.5	0.2	0.7	0.7	0.6	0.7	0.8	0.3	0.3	0.2	0.1	0.1	0.1	0.0	
1	1	High	5	Exp	0.4	2.3	1.8	2.2	1.8	5.6	3.0	1.3	0.6	0.3	0.2	0.1	0.2	0.1	0.0	0.0	0.0	0.0	0.0	0.0	D
1	1	High	5	Lin	0.2	2.4	2.8	2.1	1.7	3.8	1.9	0.8	0.4	0.1	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
3	1	High	5	Exp	0.3	1.4	1.5	1.6	1.4	3.6	1.2	0.7	0.4	0.2	0.1	0.1	0.2	0.1	0.0	0.0	0.0	0.0	0.0	0.0	D
3	1	High	5	Lin	-0.5	0.9	1.7	1.8	1.7	3.9	1.1	0.8	0.4	0.3	0.2	0.2	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
5	1	High	5	Exp	0.0	0.3	1.1	0.8	1.2	3.2	1.2	0.1	0.3	0.1	0.1	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	D
5	1	High	5	Lin	-0.2	0.3	1.4	1.3	1.6	3.8	0.5	-0.2	0.1	0.1	0.1	0.2	0.1	0.0	-0.1	0.0	0.0	0.0	0.0	0.0	
1	3	High	5	Exp	-0.6	2.2	1.5	2.0	1.3	2.5	1.7	0.6	0.5	0.2	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	D
1	3	High	5	Lin	0.4	2.5	2.0	1.9	2.3	2.2	1.2	0.8	0.6	0.2	0.1	0.1	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	
3	3	High	5	Exp	0.2	1.6	1.8	1.1	1.4	2.6	0.8	0.4	0.3	0.1	0.1	0.0	0.1	0.0	-0.1	0.0	0.0	0.0	0.0	0.0	D
3	3	High	5	Lin	-0.2	1.6	1.6	1.8	1.3	3.2	1.3	1.2	0.6	0.3	0.1	0.1	0.1	0.1	0.1	0.0	0.0	0.0	0.0	0.0	
5	3	High	5	Exp	0.1	0.3	1.0	0.9	1.1	2.6	0.3	-0.2	0.2	0.1	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	D
5	3	High	5	Lin	-0.3	0.5	1.2	1.2	1.4	3.3	0.7	0.1	0.2	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
1	5	High	5	Exp	-0.1	1.9	1.6	1.5	1.0	1.8	0.9	0.9	0.3	0.1	0.0	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	D
1	5	High	5	Lin	0.1	1.9	2.0	1.2	1.3	2.5	1.8	0.6	0.2	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
3	5	High	5	Exp	-0.5	0.8	1.1	1.2	1.3	2.3	0.7	0.3	0.3	0.1	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	D
3	5	High	5	Lin	0.3	1.0	1.2	1.6	1.3	2.4	0.2	0.3	0.2	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	
5	5	High	5	Exp	0.2	0.2	1.6	1.2	1.1	3.2	0.9	0.0	0.1	0.1	0.1	0.1	0.0	0.1	0.1	0.0	0.0	0.0	0.0	0.0	D
5	5	High	5	Lin	0.0	0.4	1.2	1.4	0.9	3.0	0.9	0.1	0.2	0.1	0.1	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	

CHAPTER IV

MEASURING ADOPTION OF INTEGRATED PEST MANAGEMENT BY COTTON GROWERS IN EASTERN NORTH CAROLINA

Abstract

Integrated Pest Management (IPM) is considered the best way for farmers to manage agricultural pests because of its focus on using multiple tactics for an optimal balance of economics, human health, and ecological soundness. Government agents and academicians typically measure the prevalence of IPM adoption by using checklists to give growers a score based on the number of IPM practices utilized. By using a survey of Eastern North Carolina cotton growers, we analyzed a typical IPM adoption scale for reliability and internal consistency. We found that growers do not approach IPM adoption as a unified concept. The practices we looked at segregated into four different components- weed management, insect management, general management, and ecosystem management- rather than a single component for IPM. This indicates that the checklist approach may not be the best method for assessing IPM adoption, especially if the researcher wants to ask more sophisticated questions such as what are the motivations for growers to adopt IPM.

Introduction

Environmental policy in the twentieth century focused largely on regulating point-source pollution, such as factory emissions. Much of the environmental policy aimed at point-source pollution was in the form of regulations and mandates (such as the Clean Air Act). Now, more attention is shifting towards non-point sources of pollution. These pose a greater challenge for regulators because the responsibility for the pollution is spread over a larger pool of stakeholders, with each stakeholder contributing a smaller portion to the overall pollution level. Additionally, non-point source pollution is a greater challenge to treat because it is dispersed throughout the environment, and thus attention is being turned to pollution prevention rather than pollution remediation.

When looking at the problem of non-point source pollution, the agricultural sector is one of the main targets for improvement due to the use of many chemicals, such as pesticides and fertilizers, applied directly to the environment. Additionally, in the agricultural sector, more so than the commercial or residential sectors, a single decision maker is responsible for large tracts of land. This means that changing the behaviors of a single grower is likely to have greater overall impacts on the environment.

The agricultural community has understood for many years their role as stewards of the environment, but in all management decisions, environmental concerns are balanced by economic and logistical concerns (Drost et al. 1996). For example, growers may prefer narrow spectrum insecticides which have fewer negative effects on non-target organisms, but are often more expensive, making it difficult to afford them, or have much narrower windows of application, making it difficult for growers to find the time to apply these targeted pesticides compared to the more toxic broad spectrum alternatives. Thus, growers are forced to balance the environment with both their finances and other resources. Individual growers must decide where that balance lies for their properties, and that has created a wide range of grower practices, with organic farmers at one end of the spectrum (Jeger 2000) and growers meeting the bare minimum environmental compliance regulations to retain federal support at the other end (Claassen et al. 2004).

One lens to look at the spectrum of grower practices is to look at the adoption of Integrated Pest Management (IPM) by growers. IPM has been defined numerously in the past forty years (Wearing 1988, Bajwa and Kogan 1997, Ehler 2006). Although it was originally coined to describe the judicious use of pesticides for the control of insect pests, more recently, IPM has been broadened to describe the management of all types of pests (insects,

weeds, pathogens, nematodes, etc.) in a manner that incorporates an understanding of the agro-ecosystem and social context of the farm. Here we define it as the combined use of chemical, biological, and cultural controls to limit insects, weeds, and diseases in a manner that minimizes risks to humans and the environment. This definition is similar to definitions used by the Environmental Protection Agency (EPA 1993) and the National Coalition on Integrated Pest Management (NCIPM 1994) because it stresses the combination of strategies for managing pests and the consideration of managing risks to both humans and the environment; other definitions stress points such as economic thresholds and information systems that are important for agricultural scientists to develop, but not as readily applicable to most growers (Bajwa and Kogan 1997).

The adoption of IPM can help reduce the volume of non-point source pollution in the forms of pesticides and fertilizers, because growers using a combination of practices for controlling pest outbreaks are likely to apply pesticides less frequently and monitor their use of fertilizers more closely to control weeds and plant pathogens. Additionally, a key IPM practice is the intentional application of chemicals that have the shortest residual times and least harmful non-target effects on wildlife and humans as possible. From an environmental standpoint, the adoption of IPM by the agricultural sector is beneficial (Ehler 2006).

Unlike organic farming, where all practices must be adhered to in order for a farm to be labeled organic, IPM can be adopted piecemeal by growers (McDonald and Glynn 1994). Some IPM practices, such as crop rotation, are almost universally adopted, while other practices, such as actively releasing biological control agents, are much less common (Malone et al. 2004). The IPM best management practices vary by crops and are continuously updated as new pest problems and technologies arise.

Because of this diversity of crops requiring unique management practices, the continually evolving nature of best management practices, and the dispersed community of growers, government is hampered in its ability to actively enforce IPM adoption (Bourguet et al. 2005). In 1993, the Clinton Administration testified before Congress that implementing IPM practices on 75% of the nation's crop acres by the year 2000 was a national goal (Jacobsen 1996), but by 2001, most state agencies were still grappling with how to measure whether a grower had adopted IPM. The state of Ohio, for example, had to create 21 different IPM definitions to account for each of their major field, fruit, and vegetable crops (Jasinski et al. 2001).

Scales for measuring IPM adoption have been published for apples in New York (Mc Donald and Glynn 1994), vegetables in California (Shennan et al. 2001), vegetables in Ohio (Jasinski et al. 2001), grain in Virginia (Malone et al. 2004), cotton in South Carolina (Robertson et al. 2005) and corn in Wisconsin (Hammond et al. 2006). In each of these cases, researchers created a checklist of IPM practices and gave growers a score based on how many practices the grower utilized. In some cases, scores were weighted so that practices considered a priori "more important" were given more weight (Shennan et al. 2001, McDonald and Glynn 1994, and Robertson et al. 2005). While many items appeared on all scales (such as monitoring fields for economic thresholds), there was a great deal of variation in the number of items on the scales and the specific points of interests on each scale. For example, the use of IPM-trained private crop consultants was a special point of interest in Shennan et al. (2001) and Hammond et al. (2006), but mostly ignored in Robertson et al. (2005).

In addition to variation in the practices included on the checklists, each study differed in how they interpreted the growers' responses. Whether growers were considered "IPM adopters" in each study varied from very specific qualifications (for example, Jasinski et al. (2001) considered growers to be IPM adopters only if they employed at least 80% of the practices on that crop's checklist), to relative rankings placing growers as low, medium, or high IPM adopters (for example, Shennan et al. 2001 considered any grower that used monitoring or thresholds to be IPM adopters with any additional practices upgrading growers to "medium" or "high" IPM adopters). This means that a grower that would be considered an IPM user in one study may not qualify in using a different scale.

As a preliminary step to addressing the question of what motivates growers to adopt a certain level of IPM, we measured IPM adoption by cotton growers in North Carolina. In trying to decide which of the available scales we should model ours on, we asked which of the scales could demonstrate that they were truly measuring the adoption of IPM and not just measuring the adoption of a collection of unrelated agricultural practices. In the social survey literature, demonstrating that all scale items measure the same underlying concept is often referred to as scale reliability or internal consistency (O'Sullivan et al. 2003). We found that only the McDonald and Glynn (1994) study had tested for internal consistency and while they claimed their scale was an accurate measure of IPM, their scale had in fact broken into nine subscales.

We created a scale of IPM adoption, using a checklist of IPM practices common in multiple scales, that was part of a larger survey on environmental attitudes. We then administered the survey to non-organic cotton growers in four eastern North Carolina counties. We analyzed our results using Cronbach's alpha and Principal Components

Analysis to demonstrate scale reliability. Because so many previous studies had used the checklist approach for measuring IPM adoption, our hypothesis was that such an approach would be a reliable measure for IPM. What we found was closer to the initial findings of McDonald and Glynn (1994), in that several items were found to be uninformative and the remaining items did not indicate a single concept of IPM, but rather four different concepts.

Methods

Data Source

The data used in this paper were part of a larger survey on environmental behaviors and attitudes by eastern North Carolina cotton growers (see Appendix for complete survey). We chose to focus on cotton growers both because cotton is a prevalent crop in North Carolina and because the economic realities of the crop make it an interesting case study. Cotton is not under the extreme quality standards that directly consumable crops (such as vegetables like tomatoes or cucumbers) face, but does have a higher economic value for quality than many field crops (such as hay or alfalfa), which means that individual growers have much more room to make decisions about the amount of pest pressure they are willing to accept and the types of management they are going to use. Additionally, cotton has many available technologies, such as transgenic varieties, that offer growers many options to chose from when deciding on a management strategy (Robertson et al. 2005).

A list of non-organic cotton growers from Edgecombe, Martin, Pitt, and Johnston Counties, NC, was compiled from extension agents' recommendations. We chose to focus on this area because Edgecombe, Martin, and Pitt Counties are amongst the top ten counties for cotton production in the state (NCDA&CS 2006), giving us a large potential population to work with. Additionally, working in this four-county area allowed us to collaborate with

another state agency interested in surveying this same population about water quality practices. Between June and August 2006, 94 growers were contacted by telephone. We asked each grower if they were the primary decision maker for the cotton operations on their farm, and if they were, would they be willing to be interviewed. If they were not the primary decision maker, we asked for contact information for that person, so that we could try to reach the primary decision maker for every farm we had contact information. Twenty-two growers agreed to be interviewed, giving us a response rate of 23.4%. This response rate was comparable to the reported response rates in other IPM surveys (24.6% in Malone et al. 2004, 21% in Robertson et al. 2005, and 22% in Hammond et al. 2006), despite the fact that our survey was an in-person interview while the other surveys were mailed to the growers. Growers were interviewed at a location of their choosing (typically in their fields), and the interviews were tape-recorded to ensure accurate transcription. Each interview took between half an hour to an hour, depending on how much the growers wished to share.

Surveyed growers' ages ranged from 29 to 66 years old (mean = 49.9) and this was highly correlated with the years the growers had been involved in farm management (R^2 = 0.779, $p < .01$), which ranged from 10 to 36 years (mean = 24.9). The distribution of ages was similar to the overall distribution of cotton growers in North Carolina, with a slightly lower average age than the state mean (~ 53 years) (USDA NASS 2002). The number of acres of cotton planted in 2005 by surveyed growers ranged from 0 to 2000, with a mean of 764.9 acres, which was similar to the overall distribution of acreage in North Carolina, with a slightly higher average acreage per farm than the state mean (~ 442 acres/farm) (USDA NASS 2002). Every surveyed grower raised multiple crops besides cotton, including various combinations of corn, soybeans, tobacco, peanuts, wheat, cantaloupes, cucumbers,

butterbeans, sweet potatoes, and rye. Because of the multi-crop nature of these farms, we feel that this survey was applicable to both cotton growers in the Southeast and farmers in North Carolina in general.

Measures

Our preliminary scale consisted of 18 items that were common to other published surveys of IPM adoption. We asked all growers if they had used each practice in the previous two growing seasons, and used the yes-no response as a binomial variable. The items (in the same wording as used in the survey) were as follows:

1. Scout your fields for insects, weeds, and diseases (Drost et al. 1996, Malone et al. 2004, McDonald and Glynn 1994, Fuglie and Kascek 2001, Jasinski et al. 2001, and Hammond et al. 2006).
2. Use economic thresholds to determine when to apply insecticides for insect control (Malone et al. 2004, McDonald and Glynn 1994, Fuglie and Kascek 2001, Jasinski et al. 2001, and Hammond et al. 2006).
3. Use economic thresholds to determine when to apply herbicides for weed control (Malone et al. 2004, McDonald and Glynn 1994, Fuglie and Kascek 2001, and Hammond et al. 2006).
4. Select insecticides, fungicides, and herbicides that have low environmental impacts (Malone et al. 2004, and McDonald and Glynn 1994).
5. Crop rotation (Drost et al. 1996, McDonald and Glynn 1994, and Jasinski et al. 2001, Hammond et al. 2006).
6. Rotate the mode of action or use multiple modes of action for herbicides (Malone et al. 2004, and Hammond et al. 2006).

7. Rotate the mode of action or use multiple modes of actions for insecticides (Malone et al. 2004, and Hammond et al. 2006).
8. Plant cover crops (Drost et al. 1996, Malone et al. 2004, and McDonald and Glynn 1994).
9. Plant buffer zones (Jasinski et al. 2001).
10. Select seeds based on drought tolerance or disease resistance (Malone et al. 2004, Jasinski et al. 2001, and Hammond et al. 2006).
11. Use biological control to reduce insects, weeds, and diseases (McDonald and Glynn 1994, Fuglie and Kascek 2001, and Hammond et al. 2006).
12. Use reduced-till, no-till, or conservation tillage (Luttrell 1994, Drost et al. 1996, Malone et al. 2004, Fuglie and Kascek 2001, Jasinski et al. 2001).
13. Time your plantings to minimize the chance of pest outbreaks (Malone et al. 2004, Jasinski et al. 2001, and Hammond et al. 2006).
14. Selectively apply pesticides in "hotspots" as opposed to blanket applications (Malone et al. 2004, McDonald and Glynn 1994, Jasinski et al. 2001, and Hammond et al. 2006).
15. Sample your soil for nutrients to fertilize to the extent needed (Drost et al. 1996, Fuglie and Kascek 2001, and Jasinski et al. 2001).
16. Contact the extension service for advice about a specific IPM problem (Jasinski et al. 2001).
17. Hire a consultant that has been trained in Integrated Pest Management (Jasinski et al. 2001, and Hammond et al. 2006).

18. Use calendar-based spraying for insects other than thrips (Malone et al. 2004, Jasinski et al. 2001, and Hammond et al. 2006).

For the first seventeen items, "yes" was marked as 1, and "no" was marked as 0. The last item was reversed scored so that "yes" was marked as 0.

Before administering the survey, we validated our survey by reviewing the items with state extension personnel that specialized in cotton production. Additionally, we reserved the first two surveys we administered as pilot studies, asking those growers to comment specifically on whether any of the questions needed clarification. Both growers had no problems with the questions used to create the scale; therefore, no changes were made to the survey, and the pilot study answers were included in the overall pool of results.

Statistical Analysis

The purpose of our scale was not to measure the total number of growers adopting IPM but to identify growers who deliberately adopted IPM from growers following conventional methods. To test the reliability of our scale of IPM adoption, we used a two-step process. First, we used Cronbach's α test to determine whether individual items contributed to the scale as a whole. Cronbach's α test examines how each item is correlated to the other items in the scale. Items that are highly correlated indicate that the items are measuring the same concept and that the scale is internally consistent; more highly correlated items result in a higher α value (O'Sullivan et al. 2003). As a preliminary step for the Cronbach's α test, we removed any scale items that had no variance (growers answered either all "yes" or all "no" for that item); because all growers claimed to do these practices, these items would be uninformative for segregating IPM adopters from non-adopters. With the remaining items, we calculated an α value for the entire scale, and also for the scale minus

each item. For any items that lowered the α value if included, we re-examined the rationale for including the item, how the item was related to other items, and the interview transcripts to see if we could justify removing the item from the scale. Any questionable items were removed and the α value was recalculated on the new scale to ensure that any items left improved the α value.

Once the scale was pared down, we used Principal Components Analysis to confirm that all the items on our scale were measuring the same concept (Kachigan 1991). If all items loaded on a single major component, we could consider that component "IPM", and be confident that our scale measured what we intended. To determine what made a component major, we rotated our principle components matrix using the varimax rotation with Kaiser normalization procedure, and accepted any component with an eigenvalue greater than one as a major component. All analyses were done using SPSS (v 10.0).

Results

We identified four items that lacked variation in response, and thus had to be removed from the scale of IPM adoption before applying Cronbach's α test. All farmers responded "yes" to items 1 (scouting fields), 2 (using economic thresholds for insects), and 15 (sampling soil for nutrients), and all farmers responded "no" to item 18 (calendar-based spraying). Once these four items were removed, we calculated a preliminary α value of 0.615. We identified five items that raised the Cronbach's α value if removed and had enough ambiguity to justify removal. Although the issue did not come up in the first two pilot surveys, it became apparent during later surveys that item 17 (hiring a consultant trained in IPM) was ambiguous. Some growers answered "no" because their consultants had not been trained in IPM (which was the intent of the question), but others answered "no" because

their consultants had not been hired but provided services as a favor (for example, one grower's brother was a consultant, and therefore was not 'hired'), and still others were confused about whether the state extension agents and chemical company representatives were considered 'consultants'. Because of the confusion, item 17 was removed from the scale.

Item 10 (selecting seeds for drought tolerance) was negatively correlated with many of the other items. The most probable reason for this was that this particular practice is not as relevant in North Carolina as it is in other parts of the country. While drought resistance is a major consideration for seed selection in the western U.S., most cotton in North Carolina does not require any more moisture than the environment provides and therefore local seed distributors do not carry such varieties (Luttrell 1994). Also, all growers responded that they use genetically modified seeds, which are only produced by a few vendors, thereby limiting the growers' ability to select on alternate traits. Because this item was likely influenced by local availability as much as deliberate choice on the part of the grower, Item 10 was removed.

Looking at the frequencies of responses, only 1 grower did not rotate his crops (Item 5). Going back to the transcript of the interview, this grower stated that he rotated crops on a four year cycle, but because the survey asked only for the most recent two years, none of his cotton acres had moved. If we credit this grower with rotating crops, there was no variation among responses; therefore, item 5 was removed.

Item 16 (contacting the extension service) had low inter-item correlation with most of the other items. Two possible factors could explain a bias in growers' responses. If one county had a disproportionately bad extension agent, then growers' willingness to contact the

extension service could be county-dependent. If no other item segregated by county, this item would have a low inter-item correlation. However, of the five "no" responses, all four counties in the survey area were represented, so this was probably not the right explanation. The other possible explanation was that the sampling frame was derived from extension agent recommendations so a) the growers surveyed may not be representative of local cotton growers at least in this respect, or b) growers could be self-reporting this incorrectly because they did not want the local extension service to think poorly of them. Because of this potential confounding factor, Item 16 was removed from the survey.

Finally, following the surveying, the frequencies of responses were brought to a cotton extension specialist. In his opinion, the responses for Item 3 (using economic thresholds for herbicides) were probably artificially inflated because there were no well published economic thresholds for the most common weeds seen in cotton. Some growers may have answered positively to that item because if they used Round-up Ready™ varieties, they never had to spray with herbicide, and therefore they used 'economic thresholds', but this was not the intent of the question. Because of this potential ambiguity, Item 3 was removed.

After making these modifications, our pared scale of IPM practices consisted of the following nine items. The resulting Cronbach's alpha was 0.614, indicating sufficient internal reliability of this scale.

- Select insecticides, fungicides, and herbicides that have low environmental impacts
- Rotate the mode of action or use multiple modes of action for herbicides
- Rotate the mode of action or use multiple modes of actions for insecticides
- Plant cover crops

- Plant buffer zones
- Use biological control to reduce insects, weeds, and diseases
- Use reduced-till, no-till, or conservation tillage
- Time your plantings to minimize the chance of pest outbreaks
- Selectively apply pesticides in "hotspots" as opposed to blanket applications

The next step for measuring the reliability of this scale was a Principle Components Analysis on the remaining nine items. The items loaded on four components having eigenvalues greater than 1. Table 1 shows the rotated component matrix. The three items loading on the first component (Selecting insecticides, fungicides, and herbicides that have low environmental impacts, rotating the mode of action or using multiple modes of action for herbicides, and using reduced-till, no-till, or conservation tillage) can be roughly categorized as "weed management" strategies. Many growers consider Round-up™ combined with Round-up Ready™ cotton as an herbicide with low environmental impacts because it reduces the total amount of chemicals applied to fields, and every grower we surveyed used a Round-up Ready™ variety of cotton. Those who also rotated the mode of action of herbicide could use reduced-tillage with little weed problems developing, but growers who relied solely on Round-up found that resistance developed if they use reduced-tillage methods without rotating the mode of action of herbicides.

The two items loading primarily on the second component (Rotating the mode or using multiple modes of action for insecticides and selectively applying pesticides in hotspots) can be categorized as "insecticide management" as both deal with insecticides. It could be argued that "selectively applying pesticides in hotspots" could also apply to herbicide treatments; however in the population we surveyed, all growers used a broadly

applied Round-up™ as their primary herbicide, so any selectively applied pesticides were insecticides.

The three items loading on the third component (Planting cover crops, planting buffer zones, and timing plantings to minimize the risk of outbreaks) can be categorized as "general management" practices. These are all actions taken by the grower that improve plant health and reduce soil erosion but do not directly impact pest populations.

The two items loading on fourth component (Planting buffer zones and using biological control) can be categorized as "ecosystem management". While buffer zones can function as an erosion prevention measure they can also serve as alternate habitat for biological control agents, which may explain why that item loaded in both components.

Overall, the four components we identified accounted for 68.8% of the total variance in responses.

Discussion

The motivation behind this study differs from many IPM studies in that it was not intending to quantify the number of growers adopting specific practices we previously defined as IPM, but rather attempt to segregate high IPM adopters from low IPM adopters using a reliable scale of IPM. By using the Cronbach's α test, we were able to pare down our scale to include only items that were meaningful indicators to our population, and by using Principle Components Analysis we were able to break the concept of IPM into components that more accurately reflect how growers themselves viewed IPM adoption. Rather than arriving at a single component that was an accurate measure of IPM, we found four components, indicating that growers do not adopt IPM as one management decision, but rather adopt IPM practices incidentally as they make decisions regarding different aspects of

their farm management. For example, a grower may be a high adopter for weed management practices but a low adopter for ecosystem management practices.

Academically, Integrated Pest Management is treated as being "integrated", but in our study, the practices that make up IPM were anything but integrated. This should not be a surprise, as other surveys that have recorded actual farmer practices have found that IPM components have been adopted in a piecemeal fashion (McDonald and Glynn 1994, Ehler 2006). However, this study goes a step further by quantitatively describing the various components of IPM as they are adopted.

While in the academic literature, IPM practices are often characterized by their method: chemical, cultural, or biological (Robertson et al. 2005), what we found was that the practices are more likely adopted based on their target: insect pests, weed pests, plant health, or ecosystem quality. Previous scales have added items from each of these components into a single IPM score, but if a score is going to be relevant for addressing further questions such as why growers do or do not adopt IPM, the components should be treated separately and scores for each component should be analyzed separately, because the growers view the practices as seperate. Similarly, our results question how comparable other scales of IPM are to each other. Although many practices show up repeatedly on different scales, each scale has its own biases for the number of practices to control insect pests, weed pests, plant health, or ecosystem quality; we found that growers that are high in one category may not be high in the other three, so scales that favor different components can rank the same grower as both "high" and "low" while both scales claim to be measuring the same concept.

Although this survey was conducted over a small geographic region and thus was limited in its scope, it identified a major gap in our understanding of IPM adoption. Surveys

that simply add up adopted practices give researchers an idea of how many practices are adopted, but not whether growers are adopting these practices as an overall IPM strategy or on a case by case basis. Our study indicates that the latter is more likely. More research into how growers actually conceive and adopt the components of IPM, rather than a single IPM strategy, will help policy makers address Ehler's concern that IPM as the academicians understand it is not presented in a way growers can use (2006).

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Table 1: Rotated Component Matrix for Adoption of IPM

	Component (variance explained)			
	Weed Management (25.6%)	Insecticide Management (18.6%)	General Management (12.9%)	Ecosystem Management (11.7%)
Did you select insecticides, fungicides, and herbicides that have low environmental impacts?	.741	-.058	-.011	.322
Did you rotate the mode of action or use multiple modes of action for herbicides?	.752	-.080	.476	.046
Did you use reduced-till, no-till, or conservation tillage?	.799	.197	-.073	-.329
Did you rotate the mode of action or use multiple modes of action for insecticides?	.194	.746	.052	.274
Did you selectively apply pesticides in hotspots?	-.129	.852	.095	-.029
Did you time your plantings to minimize the chance of pest outbreaks?	.097	.064	.828	-.162
Did you plant cover crops?	.038	.398	.513	.216
Did you plant buffer zones?	-.034	-.015	.532	.574
Did you use biological control?	.057	.260	-.118	.795

APPENDICES

A1. Computer Code for Deterministic Model

```
#pragma once
// This Program runs the Deterministic Model for Pieris rapae
// with the mortality occurring completely before oviposition.
//
// Molly Puente 11/11/2005

// First, include the relevant command libraries:
#include <iostream>
#include <cstdlib>
#include <cstdio>
#include <cmath>

//DECLARING UNIVERSAL VARIABLES- (used throughout program)
      int Induction = 0; // # induction delay days
      int Relaxation = 0; // # relaxation delay days
      double Oviposition = 0; // Oviposition rate
      int Attack = 0; // Oldest instar attacked (in days)
      double NO;// Not signaling Occupied
      double SO;// Signaling Occupied
      double SE;// Signaling Empty
      double NE;// Not signaling Empty
      double mort[21]; //This sets up the 21 stage lifetable.
      double nowpop[21]; //nowpop is current population with 1 larvae
      double doublepop[16]; // doublepop is current population that's been
      // previously infested... when it reaches 16, these individuals can
      // be grouped back with the nowpop 16 because larvae are either
      //pupated or dead.
      double futurepop[21]; // futurepop is a holding cell, the current
      //values of nowpop are referred to for both oviposition and
      //mortality, so I had to be careful not to overwrite nowpop, so
      //futurepop is a temp holding cell.
      double futuredoublepop[16]; // ditto with doublepop.
      double signal; // SO /(SO + SE)
      double random;// (SO + NO)/(SO + NO + SE + NE)
      double relevance; // signal - random

      //DECLARING OUTPUT SPACE-
      // To save data to an outside file, an Output destination
      // must be set up for each file:
      FILE *Output; //Output is for the full run summary (Output.txt)
      FILE *Output2; // Output2 is for day by day data (days.txt)
      FILE *Output3; //Outputs 3 & 4 are reserved for debugging by
      //individual plant states
      FILE *Output4;

namespace PierisOrderofOperations
{
      using namespace System;
      using namespace System::ComponentModel;
      using namespace System::Collections;
      using namespace System::Windows::Forms;
      using namespace System::Data;
      using namespace System::Drawing;
```

```
	using namespace std; // <- I add this namespace to get the system
		// screen to flash when finished running.

	/// <summary>
	/// Summary for Form1
	///
	/// WARNING: If you change the name of this class, you will need to
	/// change the 'Resource File Name' property for the managed
	/// resource compiler tool associated with all .resx files this
	/// class depends on.  Otherwise, the designers will not be able to
	/// interact properly with localized resources associated with this
	/// form.
	/// </summary>

public __gc class Form1 : public System::Windows::Forms::Form
	{
	public:
		Form1(void)
		{
			InitializeComponent();
		}

	protected:
		void Dispose(Boolean disposing)
		{
			if (disposing && components)
			{
				components->Dispose();
			}
			__super::Dispose(disposing);
		}
	private: System::Windows::Forms::Button *  Startbutton;
	private: System::Windows::Forms::TextBox *  IntoInduc;
	private: System::Windows::Forms::TextBox *  IntoRelax;
	private: System::Windows::Forms::TextBox *  IntoOvip;
	private: System::Windows::Forms::Label *  label1;
	private: System::Windows::Forms::Label *  label2;
	private: System::Windows::Forms::Label *  label3;
	private: System::Windows::Forms::GroupBox *  groupBox1;
	private: System::Windows::Forms::RadioButton *  RBFifth;
	private: System::Windows::Forms::RadioButton *  RBFourth;
	private: System::Windows::Forms::RadioButton *  RBThird;
	private: System::Windows::Forms::RadioButton *  RBSecond;
	private: System::Windows::Forms::RadioButton *  RBFirst;

	private:
		/// <summary>
		/// Required designer variable.
		/// </summary>
		System::ComponentModel::Container * components;

		/// <summary>
		/// Required method for Designer support - do not modify
		/// the contents of this method with the code editor.
		/// </summary>
```

```
void InitializeComponent(void)
{
   this->Startbutton = new System::Windows::Forms::Button();
   this->IntoInduc = new System::Windows::Forms::TextBox();
   this->IntoRelax = new System::Windows::Forms::TextBox();
   this->IntoOvip = new System::Windows::Forms::TextBox();
   this->label1 = new System::Windows::Forms::Label();
   this->label2 = new System::Windows::Forms::Label();
   this->label3 = new System::Windows::Forms::Label();
   this->groupBox1 = new System::Windows::Forms::GroupBox();
   this->RBFifth = new System::Windows::Forms::RadioButton();
   this->RBFourth = new System::Windows::Forms::RadioButton();
   this->RBThird = new System::Windows::Forms::RadioButton();
   this->RBSecond = new System::Windows::Forms::RadioButton();
   this->RBFirst = new System::Windows::Forms::RadioButton();
   this->groupBox1->SuspendLayout();
   this->SuspendLayout();
      //
      // Startbutton
      //
this->Startbutton->Location = System::Drawing::Point(24, 208);
   this->Startbutton->Name = S"Startbutton";
   this->Startbutton->Size = System::Drawing::Size(96, 32);
   this->Startbutton->TabIndex = 5;
   this->Startbutton->Text = S"Start";
   this->Startbutton->Click += new System::EventHandler(this,
      Startbutton_Click);
      //
      // IntoInduc
      //
this->IntoInduc->Location = System::Drawing::Point(16, 16);
   this->IntoInduc->Name = S"IntoInduc";
   this->IntoInduc->Size = System::Drawing::Size(80, 20);
   this->IntoInduc->TabIndex = 1;
   this->IntoInduc->Text = S"0";
      //
      // IntoRelax
      //
this->IntoRelax->Location = System::Drawing::Point(16, 40);
   this->IntoRelax->Name = S"IntoRelax";
   this->IntoRelax->Size = System::Drawing::Size(80, 20);
   this->IntoRelax->TabIndex = 2;
   this->IntoRelax->Text = S"0";
      //
      // IntoOvip
      //
this->IntoOvip->Location = System::Drawing::Point(16, 64);
   this->IntoOvip->Name = S"IntoOvip";
   this->IntoOvip->Size = System::Drawing::Size(80, 20);
   this->IntoOvip->TabIndex = 3;
   this->IntoOvip->Text = S"0.0";
      //
      // label1
      //
this->label1->Location = System::Drawing::Point(104, 16);
```

```
   this->label1->Name = S"label1";
   this->label1->Size = System::Drawing::Size(160, 24);
   this->label1->TabIndex = 13;
   this->label1->Text = S"Induction Rate (1 to 5)";
      //
      // label2
      //
this->label2->Location = System::Drawing::Point(104, 40);
   this->label2->Name = S"label2";
   this->label2->Size = System::Drawing::Size(160, 24);
   this->label2->TabIndex = 14;
   this->label2->Text = S"Relaxation Rate (1 to 5)";
      //
      // label3
      //
this->label3->Location = System::Drawing::Point(104, 64);
   this->label3->Name = S"label3";
   this->label3->Size = System::Drawing::Size(160, 24);
   this->label3->TabIndex = 15;
   this->label3->Text = S"Occupation Rate (0 to 1)";
      //
      // groupBox1
      //
this->groupBox1->Controls->Add(this->RBFifth);
   this->groupBox1->Controls->Add(this->RBFourth);
   this->groupBox1->Controls->Add(this->RBThird);
   this->groupBox1->Controls->Add(this->RBSecond);
   this->groupBox1->Controls->Add(this->RBFirst);
   this->groupBox1->Location = System::Drawing::Point(16, 88);
   this->groupBox1->Name = S"groupBox1";
   this->groupBox1->Size = System::Drawing::Size(184, 104);
   this->groupBox1->TabIndex = 4;
   this->groupBox1->TabStop = false;
   this->groupBox1->Text = S"Last Instar Attacked";
      //
      // RBFifth
      //
this->RBFifth->Location = System::Drawing::Point(48, 64);
   this->RBFifth->Name = S"RBFifth";
   this->RBFifth->Size = System::Drawing::Size(88, 24);
   this->RBFifth->TabIndex = 4;
   this->RBFifth->Text = S"5th";
      //
      // RBFourth
      //
this->RBFourth->Location = System::Drawing::Point(96, 40);
   this->RBFourth->Name = S"RBFourth";
   this->RBFourth->Size = System::Drawing::Size(80, 24);
   this->RBFourth->TabIndex = 3;
   this->RBFourth->Text = S"4th";
      //
      // RBThird
      //
this->RBThird->Location = System::Drawing::Point(96, 16);
   this->RBThird->Name = S"RBThird";
```

```
            this->RBThird->Size = System::Drawing::Size(72, 24);
            this->RBThird->TabIndex = 2;
            this->RBThird->Text = S"3rd";
               //
               // RBSecond
               //
         this->RBSecond->Location = System::Drawing::Point(8, 40);
            this->RBSecond->Name = S"RBSecond";
            this->RBSecond->Size = System::Drawing::Size(80, 24);
            this->RBSecond->TabIndex = 1;
            this->RBSecond->Text = S"2nd";
               //
               // RBFirst
               //
         this->RBFirst->Checked = true;
            this->RBFirst->Location = System::Drawing::Point(8, 16);
            this->RBFirst->Name = S"RBFirst";
            this->RBFirst->Size = System::Drawing::Size(80, 24);
            this->RBFirst->TabIndex = 0;
            this->RBFirst->TabStop = true;
            this->RBFirst->Text = S"1st";
               //
               // Form1
               //
         this->AutoScaleBaseSize = System::Drawing::Size(5, 13);
            this->ClientSize = System::Drawing::Size(288, 266);
            this->Controls->Add(this->groupBox1);
            this->Controls->Add(this->label3);
            this->Controls->Add(this->label2);
            this->Controls->Add(this->label1);
            this->Controls->Add(this->IntoOvip);
            this->Controls->Add(this->IntoRelax);
            this->Controls->Add(this->IntoInduc);
            this->Controls->Add(this->Startbutton);
            this->Name = S"Form1";
            this->Text = S"Form1";
            this->groupBox1->ResumeLayout(false);
            this->ResumeLayout(false);

         }


////////////////////////////////////////////////////////////////////////
////        Start Button Here:
////////////////////////////////////////////////////////////////////////
private: System::Void Startbutton_Click(System::Object *  sender,
      System::EventArgs *  e)
{

      Induction = System::Convert::ToInt32(IntoInduc -> Text);
      Relaxation = System::Convert::ToInt32(IntoRelax -> Text);
      Oviposition = System::Convert::ToDouble(IntoOvip -> Text);

//SET destination files that will show the data:
```

```
// ("w+" means the program can write into the destination file... If you
// want to add continuously, it's a+ for append, and if you just want to
// access, it's r+ for read-only.)
      Output=fopen("Output.txt","w+"); //Output collects summary data
      Output2 = fopen("Days.txt", "w+"); // Days collects daily totals for
      //plants
      Output3 = fopen("Plants.txt", "w+");
      Output4 = fopen("DPlants.txt", "w+");

//This Prints the header on the Output.txt:
      fprintf(Output, "%s %d \n", "The Induction Delay is ", Induction);
      fprintf(Output, "%s %d \n", "The Relaxation Delay is ", Relaxation);
      fprintf(Output, "%s %f \n", "The Oviposition Rate is ",Oviposition);

// This prints headers on the chart in Days.txt:
      fprintf(Output2, "%s %s %s %s %s %s %s %s \n","Day "," NO "," SO ",
            " SE "," NE "," Ran "," Sig "," Rel ");
      fprintf(Output3,"%s %s %s %s %s ","1 ","2 ", "3 ", "4 ", "5 ");
      fprintf(Output3, "%s %s %s %s %s %s %s %s %s %s %s %s %s %s \n",
      " 0"," 6"," 7"," 8"," 9"," 10"," 11"," 12"," 13"," 14"," 15"," 16",
      " 17"," 18");
      fprintf(Output4, "%s %s %s %s %s %s %s %s %s %s %s %s %s %s %s\n",
      " D1"," D2"," D3"," D4"," D5"," D6"," D7"," D8"," D9"," D10",
      " D11"," D12"," D13"," D14"," D15");

// This sets the oldest viable herbivore's age in days:
      if (RBFirst -> Checked) Attack = 3;
      if (RBSecond -> Checked) Attack = 6;
      if (RBThird -> Checked) Attack = 9;
      if (RBFourth -> Checked) Attack = 12;
      if (RBFifth ->Checked) Attack = 15;
      fprintf(Output, "%s %d \n", "Oldest larvae attacked is ", Attack);

//LIFE TABLE:
      mort[0] = 0; // for non occupied plants
      mort[1] = .1872; // for 1sts
      mort[2] = .1872;
      mort[3] = .1872;
      mort[4] = .0874; // for 2nds
      mort[5] = .0874;
      mort[6] = .0874;
      mort[7] = .0842; // for 3rds
      mort[8] = .0842;
      mort[9] = .0842;
      mort[10] = .1373; // for 4ths
      mort[11] = .1373;
      mort[12] = .1373;
      mort[13] = .2331; // for 5ths
      mort[14] = .2331;
      mort[15] = .2331;
      mort[16] = 0;// 16+ are plants that are abandoned but still induced
      mort[17] = 0;
      mort[18] = 0;
      mort[19] = 0;
      mort[20] = 0;
```

```
do // begins ovip rates loop.
{

//INITIALIZATION: I have to set all the values to 0 initially...
      for (int a = 0; a < 16; a++)
      {
            nowpop[a] = 0;
            doublepop[a] = 0;
            futurepop[a] = 0;
            futuredoublepop[a] = 0;
      }
      for (int a = 16; a < 22; a++)
      {
            nowpop[a] = 0;
            futurepop[a] = 0;
      }

//To start the simulation, all the plants are in the NE state:
      nowpop[0] = 100; // START with 100 plants in NE

////////////////////////////
//START DAY HERE ->     /////
////////////////////////////
      int day = 0; //day is a counter of which day it is on.
      do
      {
      //if (day>2) Oviposition=0; //Creates a pulse for debugging

      //MORTALITY and MATURATION:
      //The dead stay dead:
            futurepop[0] = futurepop[0] + nowpop[0];
      //Everything in the NO, will either mature to next step or die to 0:
            for(int i= 1; i <= Induction; i++)
            {
              futurepop[0] = futurepop[0] + mort[i] * nowpop[i];
              futurepop[i+1] = futurepop[i+1] + (1-mort[i]) * nowpop[i];
            }
      //Everything in SO, will either mature to next step or die to 16:
            for(int i = (Induction + 1); i < 16; i++)
            {
              futurepop[16] = futurepop[16] + mort[i] * nowpop[i];
              futurepop[i+1] = futurepop[i+1] + (1 - mort[i]) * nowpop[i];
            }
      //Everything in used SO, will mature to next step or die to 16:
      for(int i = 1; i < 15; i++)
            {
              futurepop[16] = futurepop[16] + mort[i] * doublepop[i];
              futuredoublepop[i+1] = futuredoublepop[i+1] + (1-mort[i]) *
                  doublepop[i];
            }
      //Both pupating and dying D15's go onto level 16.
            futurepop[16] = futurepop[16] + doublepop[15];
      //Everything in SE will mature to next step (no death).
            for(int i = 16; i < (15 + Relaxation); i++) futurepop[i+1] =
                  futurepop[i+1] + nowpop[i];
```

```
//Things that need to be turned off relaxation:
      futurepop[0] = futurepop[0] + nowpop[15 + Relaxation];

//UPDATE all plants before oviposition:
   for (int c = 0; c <= 20; c++) nowpop[c] = futurepop[c];
   for (int c = 0; c <= 20; c++) futurepop[c] = 0;
   for (int c = 1; c <= 15; c++) doublepop[c] = futuredoublepop[c];
   for (int c = 1; c <= 15; c++) futuredoublepop[c] = 0;
   fprintf(Output3,"%f ", nowpop[0]);
   for(int c = 1; c <= 5; c++) fprintf(Output3,"%f ", nowpop[c]);
   //fprintf(Output3," \n");
   for (int c = 6; c <= 20; c++)fprintf(Output3,"%f ", nowpop[c]);
   fprintf(Output3," %s \n", "M");
   for (int c = 1; c <= 15; c++)fprintf(Output4,"%f ",
      doublepop[c]);
   fprintf(Output4," %s \n", "M");

//OVIPOSITION:
// Everything not currently induced gets set to pop[1]:
      for (int i = 0; i <= Induction; i++)
      {
         futurepop[1] = futurepop[1] + Oviposition * nowpop[i];
         futurepop[i] = futurepop[i] + (1-Oviposition) * nowpop[i];
      }
//Already signaling plants get sent to purgatory...doublepop[1];
      for(int i = (Induction + 1); i <= (15+Relaxation); i++)
      {
         futuredoublepop[1] = futuredoublepop[1] + Oviposition *
            nowpop[i];
         futurepop[i] = futurepop[i] + (1-Oviposition) * nowpop[i];
      }
      for (int i = 1; i <= 15; i++)
      {
         futuredoublepop[1] = futuredoublepop[1] + Oviposition
            *doublepop[i];
         futuredoublepop[i] = futuredoublepop[i] + (1-Oviposition) *
            doublepop[i];
      }

//UPDATE all plants before reckoning:
      for (int c = 0; c <= 20; c++) nowpop[c] = futurepop[c];
      for (int c = 0; c <= 20; c++) futurepop[c] = 0;
      for (int c = 1; c <= 15; c++) doublepop[c] =
            futuredoublepop[c];
      for (int c = 1; c <= 15; c++) futuredoublepop[c] = 0;
      fprintf(Output3,"%f ", nowpop[0]);
      for(int c = 1; c <= 5; c++) fprintf(Output3,"%f ", nowpop[c]);
      //fprintf(Output3," \n");
      for (int c = 6; c <= 20; c++)fprintf(Output3,"%f ",nowpop[c]);
      fprintf(Output3," %s \n", "Ovip");
      for (int c = 1; c <= 15; c++)fprintf(Output4,"%f ",
            doublepop[c]);
      fprintf(Output4," %s \n", "Ovip");
```

```
//Now to convert plants to occupation states:
      SE = 0; //SE = signaling empty ~[16-Relax]
      SO = 0;// SO = signaling occupied ~[ind - 16]
      NO = 0;// NO = Notsignaling occupied ~[1-ind]
      NE = nowpop[0]; //NE = Notsignaling empty... always pop[0]

// Determining if something is occupied depends on what stages of
// larvae a wasp can attack.
      Attack = 0;
      if (RBFirst -> Checked) //RBs are radio buttons on user screen
      {
            Attack = 3;
            if (Attack < Induction)
            {
            //the plants considered occupied are not induced yet,
            // unless the plant was already induced.
            for(int g = 1; g <= Attack; g++) NO = NO + nowpop[g];
            for(int g = 1; g <= Attack; g++) SO = SO + doublepop[g];
            NE = nowpop[0];
            for(int g = Attack + 1; g <= Induction; g++) NE = NE +
                  nowpop[g];
            for(int g = (Induction + 1); g <= 20; g++) SE = SE +
                  nowpop[g]; //
            for(int g = Attack + 1; g <= 15; g++) SE = SE +
                  doublepop[g];
            }
            if (Attack > Induction)
            {
            // the occupied plants could be either signaling or
            // not...
            NE = nowpop[0];
            for(int h = 1; h <= Induction; h++) NO = NO + nowpop[h];
            for(int h = Induction + 1; h <= Attack; h++) SO = SO +
                  nowpop[h];
            for(int h = 1; h <= Attack; h++) SO = SO + doublepop[h];
            for(int h = Attack + 1; h <= 20; h++) SE = SE +
                  nowpop[h];
            for(int h = Attack + 1; h <= 15; h++) SE = SE +
                  doublepop[h];
            }
            if (Attack == Induction)
            {
            NE = nowpop[0];
            for(int j = 1; j <= Attack; j++) NO = NO + nowpop[j];
            for(int j = 1; j <= Attack; j++) SO = SO + doublepop[j];
            for(int j = Attack + 1; j <= 20; j++) SE = SE +
                  nowpop[j];
            for(int j = Attack + 1; j <= 15; j++) SE = SE +
                  doublepop[j];
            }
      }
      if (RBSecond -> Checked)
      {
            Attack = 6;
            NE = nowpop[0];
```

```
            for(int h = 1; h <= Induction; h++) NO = NO + nowpop[h];
            for(int h = Induction + 1; h <= Attack; h++) SO = SO +
                  nowpop[h];
            for(int h = 1; h <= Attack; h++) SO = SO + doublepop[h];
            for(int h = Attack + 1; h <= 20; h++) SE = SE +
                  nowpop[h];
            for(int h = Attack + 1; h <= 15; h++) SE = SE +
                  doublepop[h];
      }
      if (RBThird -> Checked)
      {
            Attack = 9;
            NE = nowpop[0];
            for(int h = 1; h <= Induction; h++) NO = NO + nowpop[h];
            for(int h = Induction + 1; h <= Attack; h++) SO = SO +
                  nowpop[h];
            for(int h = 1; h <= Attack; h++) SO = SO + doublepop[h];
            for(int h = Attack + 1; h <= 20; h++) SE = SE +
                  nowpop[h];
            for(int h = Attack + 1; h <= 15; h++) SE = SE +
                  doublepop[h];
      }
      if (RBFourth -> Checked)
      {
            Attack = 12;
            NE = nowpop[0];
            for(int h = 1; h <= Induction; h++) NO = NO + nowpop[h];
            for(int h = Induction + 1; h <= Attack; h++) SO = SO +
                  nowpop[h];
            for(int h = 1; h <= Attack; h++) SO = SO + doublepop[h];
            for(int h = Attack + 1; h <= 20; h++) SE = SE +
                  nowpop[h];
            for(int h = Attack + 1; h <= 15; h++) SE = SE +
                  doublepop[h];
      }
      if (RBFifth -> Checked)
      {
            Attack = 15;
            NE = nowpop[0];
            for(int h = 1; h <= Induction; h++) NO = NO + nowpop[h];
            for(int h = Induction + 1; h <= Attack; h++) SO = SO +
                  nowpop[h];
            for(int h = 1; h <= Attack; h++) SO = SO + doublepop[h];
            for(int h = Attack + 1; h <= 20; h++) SE = SE +
                  nowpop[h];
      }
      signal = (SO) / (SO + SE);
      random = (SO + NO) / (SE + SO + NO + NE);
      relevance = signal - random;
      fprintf(Output2, "%d %f %f %f %f %f %f %f \n", day, NO, SO,
            SE, NE, random, signal, relevance);

      day++;
} while (day <= 100); // <- ENDS DAY HERE
```

```
      fprintf(Output, "%f %f %f %f %f %f %f \n", Oviposition, NO, SO, SE,
            NE, signal, random);
      Oviposition = Oviposition + 0.1;
} while (Oviposition < 1.0);

fclose(Output); //data
fclose(Output2); // Days
fclose(Output3); // Plants
fclose(Output4); // DPlants
system("PAUSE");

} //ends START button

};
}
```

A2. Computer Code for Stochastic Model

```
#pragma once
// BUM Foraging Model is the final draft of the spatially-explicit,
// stochastic simulation model for Pieris rapae.
//
// Molly Puente 1/31/07

// INCLUDE NECESSARY LIBRARIES:
#include <iostream>
#include <cstdlib>
#include <cstdio>
#include <cmath>
#include <list>


/******* RANDOM NUMBER GENERATOR BY ZIFF (via Krisztian)***/
#include <ctime>
extern int rand();
extern void srand();

#define A 471
#define B 1586
#define C 6988
#define D 9689
#define M 16383
#define RIMAX 2147483648.0        /* = 2^31 */
#define RandomInteger (++nd, ra[nd & M] = ra[(nd-A) & M] ^ ra[(nd-B) & M]
^ ra[(nd-C) & M] ^ ra[(nd-D) & M])
void seed(long seed);
static long ra[M+1], nd;

void seed(long seed) // the seed is for the random number generator
{
  int  i;

  if(seed<0) { puts("SEED error."); exit(1); }
  ra[0]= (long) fmod(16807.0*(double)seed, 2147483647.0);
  for(i=1; i<=M; i++)
  {
    ra[i] = (long)fmod( 16807.0 * (double) ra[i-1], 2147483647.0);
  }
}
/********** END OF RANDOM GENERATOR BY ZIFF **************/

//DECLARING VARIABLES-
// Initially inputted by user:
      int Induction = 0; // # induction delay days
      int Relaxation = 0; // # relaxation delay days
      int Oviposition = 0; // Oviposition rate
      int Attack = 0; // Oldest instar attacked
      int Runs = 0; // Runs is the total number of runs for each start
      //button
      int Rowsize = 0; // Rowsize is the # plants/row
      int Days = 100; // Number of days (loops) the program is run for
```

```
// Defined within the program:
      double mort[29]; //mort is the array of the life table
      int Totalplants; // Totalplants is Rowsize squared, and the # plants
      // in the field
      int age; // holding place for the age of each herbivore
      int day; // counter for the daystep
      int newplants; //newplants are the number of plants that need to be
      // oviposited on
      int runs; //counter for the current run
      int location; // holds the next random location for egg placement
      bool eggyet; // Stores whether a plant has an egg yet or not.
      int NO = 0; // count of Not Signaling Occupied
      int SO = 0; // count of Signaling Occupied
      int SE = 0; // count of Signaling Empty
      int NE = 0; // count of Not Signaling Empty
      int Frustration; // Counts the number of filled plants each
      //butterfly encounters
      double fifthday; // The remainder of day/5

// Wasp foraging parameters:
      double Flight = 3.0; // (value for a (flight speed) in seconds/m)
      double HandleTime = 13.1; // (value for b (handling time) in
      //seconds/host encountered)
      double Giveup = 73.5; // (value for c (givingup time) in
      //seconds/plant)
      int TIME = 3600; // (value for Tt (total foraging time) in seconds)
      int xdist = 0; // used for calculating wasp distance travelled
      //(left/right)
      int ydist = 0; // used for calculating wasp distance travelled
      //(up/down)
      int wasplocation = 0; //this is the current location of the wasp
      //when tracing its path
      double wasptime = 0; // this is the calculator for how much time the
      //wasp has used up so far
      int AvailablePlants[400]; //this is the picking list for randomly
      //foraging wasps
      int AvailableSignal[400]; //this is the picking list for signal
      //foraging wasps
      int targetplant; //This is a place holder for creating the list
      int nextavail; // counter for filling in the available array
      int FlyBias[5]; // array for the movement distance bias for wasps
      int TotalAvailPlants; //size of bias array
      int WaspPath[50]; //follows wasps' path
      bool NextPlant; //check to see if wasp ready to move on
      int Picker; // randomly picked plant
      int WaspDistance; //calculation of the linear distance for wasp
      //movement
      int Visitcounter; // counter for filling the WaspPath array
      int PreviousPlant; // holder used for calculating distances traveled

// INSERT PLANT STRUCTURE HERE:
      struct Field //Each plant in the field is defined by certain
      //characteristics
      {
```

```
            int row; //row indicates which row the plant is on (0-19)
            int column; // column indicates which column (0-19)
            int induction; // induction is the strength of induction(0 =
            //no induction)
            int herbivore[20]; //There can be 20 herbivores (0-19) and
            //each has a certain age that will fill in the space (0 =
            //empty; 1-28 = larval age)
            int relaxdelay; //this counts the days for the on off delay.
            int parasitism[20]; // Each herbivore position has the
            // possibility of being parasitized. C. rubecula hatch out of
            //fourth instars (day 17)(Jones et al 1987)
            // (0 = unparasitized, 1-17 = time since parasitization)
            bool occupied; // if the plant has any larvae, it gets flagged
            //as 1
      };
      Field plant[10000]; //<- sets the max field size to 100x100

// INSERT DAILY LOG STRUCTURE HERE:
      struct Calendar
      {
            int eggs;
            int firsts;
            int seconds;
            int thirds;
            int fourths;
            int fifths;
            int pupae;
            int pfirsts; //Those with "p" are for parasitized
            int pseconds;
            int pthirds;
            int pfourths;
            int pfifths;
            int newadults;
            int adults;
            int waspeggs;
            int plantsvisited;
      };
      Calendar dailylog[101];


//DECLARING OUTPUT SPACE-
      FILE *Output1; // Output1 = input.txt to double check that values
      //were read correctly
      FILE *Output2; // Output2 = data.txt gives plant details for 1 run
      FILE *Output3; // Output3 = runs.txt summarizes data for group of
      //runs
      FILE *Output4; // Output4 = herbivore.txt gives daily summary for
      //herbivore population
      FILE *Output5; // Output5 = statistics.txt gives the spatial
      //statistics calculations
      FILE *Output6; // Output6 = WaspCatch.txt gives the wasp run data

namespace BUMForagingModel
{
      using namespace System;
```

```
	using namespace System::ComponentModel;
	using namespace System::Collections;
	using namespace System::Windows::Forms;
	using namespace System::Data;
	using namespace System::Drawing;
	using namespace std;

	/// <summary>
	/// Summary for Form1
	///
	/// WARNING: If you change the name of this class, you will need to
	/// change the 'Resource File Name' property for the managed
	/// resource compiler tool associated with all .resx files this
	/// class depends on.  Otherwise, the designers will not be able to
	/// interact properly with localized resources associated with this
	/// form.
	/// </summary>

public __gc class Form1 : public System::Windows::Forms::Form
	{
	public:
	Form1(void)
	{
		InitializeComponent();
	}

	protected:
	void Dispose(Boolean disposing)
	{
		if (disposing && components)
		{
			components->Dispose();
		}
		__super::Dispose(disposing);
	}
	private: System::Windows::Forms::TextBox *  IntoInduc;
	private: System::Windows::Forms::Label *  label1;
	private: System::Windows::Forms::TextBox *  IntoRelax;
	private: System::Windows::Forms::Label *  label2;
	private: System::Windows::Forms::Label *  label3;
	private: System::Windows::Forms::Label *  label4;
	private: System::Windows::Forms::Label *  label5;
	private: System::Windows::Forms::Label *  label6;
	private: System::Windows::Forms::GroupBox *  groupBox1;
	private: System::Windows::Forms::Button *  button1;
	private: System::Windows::Forms::TextBox *  IntoOvip;
	private: System::Windows::Forms::TextBox *  IntoDays;
	private: System::Windows::Forms::TextBox *  IntoField;
	private: System::Windows::Forms::TextBox *  IntoRuns;
	private: System::Windows::Forms::RadioButton *  RB5;
	private: System::Windows::Forms::RadioButton *  RB4;
	private: System::Windows::Forms::RadioButton *  RB3;
	private: System::Windows::Forms::RadioButton *  RB2;
	private: System::Windows::Forms::RadioButton *  RB1;
```

```
private: System::Windows::Forms::GroupBox *  groupBox2;
private: System::Windows::Forms::RadioButton *  RBRandom;
private: System::Windows::Forms::RadioButton *  RBSignal;
private:
      /// <summary>
      /// Required designer variable.
      /// </summary>
System::ComponentModel::Container * components;

      /// <summary>
      /// Required method for Designer support - do not modify
      /// the contents of this method with the code editor.
      /// </summary>
void InitializeComponent(void)
{
      this->IntoInduc = new System::Windows::Forms::TextBox();
      this->label1 = new System::Windows::Forms::Label();
      this->IntoRelax = new System::Windows::Forms::TextBox();
      this->label2 = new System::Windows::Forms::Label();
      this->IntoOvip = new System::Windows::Forms::TextBox();
      this->label3 = new System::Windows::Forms::Label();
      this->IntoDays = new System::Windows::Forms::TextBox();
      this->label4 = new System::Windows::Forms::Label();
      this->IntoField = new System::Windows::Forms::TextBox();
      this->label5 = new System::Windows::Forms::Label();
      this->IntoRuns = new System::Windows::Forms::TextBox();
      this->label6 = new System::Windows::Forms::Label();
      this->groupBox1 = new System::Windows::Forms::GroupBox();
      this->RB5 = new System::Windows::Forms::RadioButton();
      this->RB4 = new System::Windows::Forms::RadioButton();
      this->RB3 = new System::Windows::Forms::RadioButton();
      this->RB2 = new System::Windows::Forms::RadioButton();
      this->RB1 = new System::Windows::Forms::RadioButton();
      this->button1 = new System::Windows::Forms::Button();
      this->groupBox2 = new System::Windows::Forms::GroupBox();
      this->RBSignal = new System::Windows::Forms::RadioButton();
      this->RBRandom = new System::Windows::Forms::RadioButton();
      this->groupBox1->SuspendLayout();
      this->groupBox2->SuspendLayout();
      this->SuspendLayout();
            //
            // IntoInduc
            //
      this->IntoInduc->Location = System::Drawing::Point(8, 16);
      this->IntoInduc->Name = S"IntoInduc";
      this->IntoInduc->Size = System::Drawing::Size(64, 20);
      this->IntoInduc->TabIndex = 0;
      this->IntoInduc->Text = S"0";
            //
            // label1
            //
      this->label1->Location = System::Drawing::Point(80, 16);
      this->label1->Name = S"label1";
      this->label1->Size = System::Drawing::Size(144, 32);
```

```
this->label1->TabIndex = 1;
this->label1->Text = S"Induction Rate (1-5)";
      //
      // IntoRelax
      //
this->IntoRelax->Location = System::Drawing::Point(8, 48);
this->IntoRelax->Name = S"IntoRelax";
this->IntoRelax->Size = System::Drawing::Size(64, 20);
this->IntoRelax->TabIndex = 2;
this->IntoRelax->Text = S"0";
      //
      // label2
      //
this->label2->Location = System::Drawing::Point(80, 48);
this->label2->Name = S"label2";
this->label2->Size = System::Drawing::Size(144, 32);
this->label2->TabIndex = 3;
this->label2->Text = S"Relaxation Rate (1-5)";
      //
      // IntoOvip
      //
this->IntoOvip->Location = System::Drawing::Point(8, 80);
this->IntoOvip->Name = S"IntoOvip";
this->IntoOvip->Size = System::Drawing::Size(64, 20);
this->IntoOvip->TabIndex = 4;
this->IntoOvip->Text = S"0";
      //
      // label3
      //
this->label3->Location = System::Drawing::Point(80, 80);
this->label3->Name = S"label3";
this->label3->Size = System::Drawing::Size(144, 32);
this->label3->TabIndex = 5;
this->label3->Text = S"Oviposition rate (eggs/butterfly)";
      //
      // IntoDays
      //
this->IntoDays->Location = System::Drawing::Point(248, 16);
this->IntoDays->Name = S"IntoDays";
this->IntoDays->Size = System::Drawing::Size(56, 20);
this->IntoDays->TabIndex = 6;
this->IntoDays->Text = S"100";
      //
      // label4
      //
this->label4->Location = System::Drawing::Point(312, 16);
this->label4->Name = S"label4";
this->label4->Size = System::Drawing::Size(128, 24);
this->label4->TabIndex = 7;
this->label4->Text = S"Season Length";
      //
      // IntoField
      //
this->IntoField->Location = System::Drawing::Point(248, 48);
this->IntoField->Name = S"IntoField";
```

```
this->IntoField->Size = System::Drawing::Size(56, 20);
this->IntoField->TabIndex = 8;
this->IntoField->Text = S"20";
      //
      // label5
      //
this->label5->Location = System::Drawing::Point(312, 48);
this->label5->Name = S"label5";
this->label5->Size = System::Drawing::Size(128, 24);
this->label5->TabIndex = 9;
this->label5->Text = S"Plants/Row";
      //
      // IntoRuns
      //
this->IntoRuns->Location = System::Drawing::Point(248, 80);
this->IntoRuns->Name = S"IntoRuns";
this->IntoRuns->Size = System::Drawing::Size(56, 20);
this->IntoRuns->TabIndex = 10;
this->IntoRuns->Text = S"1";
      //
      // label6
      //
this->label6->Location = System::Drawing::Point(312, 80);
this->label6->Name = S"label6";
this->label6->Size = System::Drawing::Size(128, 24);
this->label6->TabIndex = 11;
this->label6->Text = S"Number of Runs";
      //
      // groupBox1
      //
this->groupBox1->Controls->Add(this->RB5);
this->groupBox1->Controls->Add(this->RB4);
this->groupBox1->Controls->Add(this->RB3);
this->groupBox1->Controls->Add(this->RB2);
this->groupBox1->Controls->Add(this->RB1);
this->groupBox1->Location = System::Drawing::Point(16, 128);
this->groupBox1->Name = S"groupBox1";
this->groupBox1->Size = System::Drawing::Size(192, 160);
this->groupBox1->TabIndex = 12;
this->groupBox1->TabStop = false;
this->groupBox1->Text = S"Oldest Instar Attacked";
      //
      // RB5
      //
this->RB5->Location = System::Drawing::Point(16, 120);
this->RB5->Name = S"RB5";
this->RB5->TabIndex = 4;
this->RB5->Text = S"Fifths";
      //
      // RB4
      //
this->RB4->Location = System::Drawing::Point(16, 96);
this->RB4->Name = S"RB4";
this->RB4->TabIndex = 3;
this->RB4->Text = S"Fourths";
```

```
            //
            // RB3
            //
this->RB3->Location = System::Drawing::Point(16, 72);
this->RB3->Name = S"RB3";
this->RB3->TabIndex = 2;
this->RB3->Text = S"Thirds";
            //
            // RB2
            //
this->RB2->Location = System::Drawing::Point(16, 48);
this->RB2->Name = S"RB2";
this->RB2->TabIndex = 1;
this->RB2->Text = S"Seconds";
            //
            // RB1
            //
this->RB1->Checked = true;
this->RB1->Location = System::Drawing::Point(16, 24);
this->RB1->Name = S"RB1";
this->RB1->TabIndex = 0;
this->RB1->TabStop = true;
this->RB1->Text = S"Firsts";
            //
            // button1
            //
this->button1->Location = System::Drawing::Point(296, 264);
this->button1->Name = S"button1";
this->button1->Size = System::Drawing::Size(80, 32);
this->button1->TabIndex = 16;
this->button1->Text = S"Start";
this->button1->Click += new System::EventHandler(this,
            button1_Click);
            //
            // groupBox2
            //
this->groupBox2->Controls->Add(this->RBSignal);
this->groupBox2->Controls->Add(this->RBRandom);
this->groupBox2->Location = System::Drawing::Point(232, 136);
this->groupBox2->Name = S"groupBox2";
this->groupBox2->Size = System::Drawing::Size(192, 104);
this->groupBox2->TabIndex = 15;
this->groupBox2->TabStop = false;
this->groupBox2->Text = S"Foraging";
            //
            // RBSignal
            //
this->RBSignal->Location = System::Drawing::Point(16, 40);
this->RBSignal->Name = S"RBSignal";
this->RBSignal->Size = System::Drawing::Size(144, 24);
this->RBSignal->TabIndex = 1;
this->RBSignal->Text = S"Signal Foraging";
            //
            // RBRandom
            //
```

```
            this->RBRandom->Checked = true;
            this->RBRandom->Location = System::Drawing::Point(16, 16);
            this->RBRandom->Name = S"RBRandom";
            this->RBRandom->Size = System::Drawing::Size(144, 24);
            this->RBRandom->TabIndex = 0;
            this->RBRandom->TabStop = true;
            this->RBRandom->Text = S"Random Foraging";
                  //
                  // Form1
                  //
            this->AutoScaleBaseSize = System::Drawing::Size(5, 13);
            this->ClientSize = System::Drawing::Size(576, 406);
            this->Controls->Add(this->groupBox2);
            this->Controls->Add(this->button1);
            this->Controls->Add(this->groupBox1);
            this->Controls->Add(this->label6);
            this->Controls->Add(this->IntoRuns);
            this->Controls->Add(this->label5);
            this->Controls->Add(this->IntoField);
            this->Controls->Add(this->label4);
            this->Controls->Add(this->IntoDays);
            this->Controls->Add(this->label3);
            this->Controls->Add(this->IntoOvip);
            this->Controls->Add(this->label2);
            this->Controls->Add(this->IntoRelax);
            this->Controls->Add(this->label1);
            this->Controls->Add(this->IntoInduc);
            this->Name = S"Form1";
            this->Text = S"Form1";
            this->groupBox1->ResumeLayout(false);
            this->groupBox2->ResumeLayout(false);
            this->ResumeLayout(false);
      }

////////////////////////////////////////////////
////   START BUTTON HERE:
////////////////////////////////////////////////
private: System::Void button1_Click(System::Object *  sender,
System::EventArgs *  e)
{
//READ in variables from the form:
      Induction = System::Convert::ToInt32(IntoInduc -> Text);
      Relaxation = System::Convert::ToInt32(IntoRelax -> Text);
      Oviposition = System::Convert::ToInt32(IntoOvip -> Text);
      Runs = System::Convert::ToInt32(IntoRuns -> Text);
      Rowsize = System::Convert::ToInt32(IntoField -> Text);
      Days = System::Convert::ToInt32(IntoDays -> Text);

// Output1 reaffirms what the initial inputs and parameters were:
      Output1 = fopen("Input.txt","w+");
      if (RB1 ->Checked) Attack = 8;
      if (RB2 ->Checked) Attack = 11;
      if (RB3 ->Checked) Attack = 14;
      if (RB4 ->Checked) Attack = 17;
      if (RB5 ->Checked) Attack = 20;
```

```
      fprintf(Output1, "%s %d \n", "The Induction Delay is ", Induction);
      fprintf(Output1, "%s %d \n", "The Relaxation Delay is ",
            Relaxation);
      fprintf(Output1, "%s %d \n", "The Oviposition Rate is ",
            Oviposition);
      fprintf(Output1, "%s %d \n", "The Number of Runs is ", Runs);
      fprintf(Output1, "%s %d \n", "The Field Dimensions are ", Rowsize);
      fprintf(Output1, "%s %d \n", "The Oldest Herbi Attacked is ",
            Attack);
      fclose(Output1);
      // End READING in variables

//CREATE OUTPUT FILES:
      Output3 = fopen("runs.txt", "w+");
      Output5 = fopen("statistics.txt", "w+");
      Output6 = fopen("WaspsCatch.txt", "w+");

// <- IF CREATING MULTIPLE RUNS START HERE:
for (int runs = 1; runs <= Runs; runs++) // change # runs here
{
      Output2 = fopen("data.txt","w+");
      Output4 = fopen("herbivore.txt","w+");
      fprintf(Output4, "%s %s %s %s %s \n", "Day: "," Egg"," Larvae 1-5
            Sum/Para."," Pupa"," Adult");
      fprintf(Output5, "%s %d \n", "Run: ", runs);
      fprintf(Output6, "%s %d \n", "Run: ", runs);
      fprintf(Output3, "%s %d \n", "Run: ", runs);
      fprintf(Output3, "%s %s %s %s %s \n", "Day ", "NO "," SO ", " SE ",
            " NE ");

      seed(time(0)); //sets the random number generator to the clock.


//INITIALIZING VARIABLES:

//INSERT LIFE TABLE HERE:
//Pieris rapae can exist in several states. An unparasitized rapae still
//attached to a plant, is in states 1-28, with mortality defined here:
      mort[0] = 0; // age 0 is an empty larva set
      mort[1] = 0.0235; // ages 1-5 are eggs
      mort[2] = 0.0235;
      mort[3] = 0.0235;
      mort[4] = 0.0235;
      mort[5] = 0.0235;
      mort[6] = 0.1872; // ages 6-8 are 1st instars
      mort[7] = 0.1872;
      mort[8] = 0.1872;
      mort[9] = 0.0872; // ages 9-11 are 2nd instars
      mort[10] = 0.0872;
      mort[11] = 0.0872;
      mort[12] = 0.0842; // ages 12-14 are 3rd instars
      mort[13] = 0.0842;
      mort[14] = 0.0842;
      mort[15] = 0.1373; // ages 15-17 are 4th instars
      mort[16] = 0.1373;
```

```
      mort[17] = 0.1373;
      mort[18] = 0.2331; // ages 18-20 are 5th instars
      mort[19] = 0.2331;
      mort[20] = 0.2331;
      mort[21] = 0.0074; // ages 21-28 are pupae
      mort[22] = 0.0074;
      mort[23] = 0.0074;
      mort[24] = 0.0074;
      mort[25] = 0.0074;
      mort[26] = 0.0074;
      mort[27] = 0.0074;
      mort[28] = 0.0074;
//All larvae moving into state 29 have hatched from pupae, and thus have
//become ADULTS, and move into that category.

      Totalplants = Rowsize * Rowsize;
// In order to have a flexible field size, I need to assign the rows and
//columns based on user input
      int a = 0;
      do //this loop assigns each plant a place in the field
      {
            for (int b = 0; b < Rowsize; b++)
            {
               for (int c = 0; c < Rowsize; c++)
               {
                  plant[a].row = b;
                  plant[a].column = c;
                  a = a + 1;
               } //ends columns
            } // ends rows
      } while (a < Totalplants);

      for (int a = 0; a < Totalplants; a++)// This loop starts the empty
      //field
      {
            plant[a].induction = 0; // initially no signal
            plant[a].relaxdelay = 0; //This line is just for On/Off delay
            //initially
            plant[a].occupied = 0;
            for (int b = 0; b < 20; b++)
            {
                  plant[a].herbivore[b] = 0; // initially no herbis
                  plant[a].parasitism[b] = 0; // no herbis means no
                  //parasitism
            }
      }//end field initialization

      for (int d = 0; d <= Days; d++)
      {
            dailylog[d].eggs = 0;
            dailylog[d].firsts = 0;
            dailylog[d].seconds = 0;
            dailylog[d].thirds = 0;
            dailylog[d].fourths = 0;
            dailylog[d].fifths = 0;
```

```
            dailylog[d].pupae = 0;
            dailylog[d].pfirsts = 0;
            dailylog[d].pseconds = 0;
            dailylog[d].pthirds = 0;
            dailylog[d].pfourths = 0;
            dailylog[d].pfifths = 0;
            dailylog[d].newadults = 0;
            dailylog[d].adults = 0;
            dailylog[d].waspeggs = 0;
            dailylog[d].plantsvisited = 0;
      }

//START DAY HERE:
////////////////////////////////////////////////////////
      day = 0;
      for (day = 0; day <= Days; day++)
      {
            fifthday = fmodf(day,5);
            if(fifthday == 0) fprintf(Output2,"%s %d \n", "day: ", day);
            fprintf(Output4,"%d  ", day );


            dailylog[0].newadults = 1; // initially there has to be 1
            //adult.

      //Mortality & Maturation: NOT PARASITIZED)

            for(int f = 0; f < Totalplants; f++) //plant counter
            {
               for(int g = 0; g < 20; g++) //herbivore counter
               {
                  age = 0;
                  age = plant[f].herbivore[g]; //sets age to herbivore age
                  plant[f].parasitism[g] = 0; //sets all parasitism flags
                  //to zero
                  double r5 = ((double) RandomInteger/RIMAX); //pulls a
                  //random integer
                  if(r5 <= mort[age]) // If the random # is <= the
                  //mortality for that age class, the larva dies, and its
                  //spot is opened up (set to 0)
                  {
                     plant[f].herbivore[g] = 0; //MORTALITY
                  }
                  age = plant[f].herbivore[g]; //Resets age in case of
                  //death
                  if(age != 0) plant[f].herbivore[g] = age + 1;
                  //MATURATION
                  // for all eggs, larv., and pupa, they get aged 1 day.
                  if(age == 28) //This is survival of pupae to adulthood
                  {
                     plant[f].herbivore[g] = 0; // the spot is opened up
                     dailylog[day].newadults += 1; //non-parasitized pupae
                     //become adults
                  }// ends pupae maturation
```

```
            }// end herbivore (g loop)
          }// end plant (f loop)
      if (day == 0) dailylog[day].adults += dailylog[day].newadults;
      if (day > 0)
      {
            dailylog[day].newadults = 0.5 * dailylog[day].newadults;
            // half the value to get rid of males
            dailylog[day].adults = dailylog[day-1].adults +
                  dailylog[day].newadults;
            // newadults are added into entire adult pop.
      }
      if (day >= 21) dailylog[day].adults -= dailylog[day - 21].newadults;
      // Adults die after 3 weeks.

//OVIPOSITION SUBROUTINE HERE: from Jones 1977
      double ZERO = 0.32; //ZERO is the prob of a butterfly not moving
      double MOVE1 = 0.2; //MOVE1 is the prob of moving in the favored
      //direction
      double MOVE2 = 0.375; // p(45 degrees clkwise) = 0.175
      double MOVE3 = 0.55; //p(45 degrees counterclkwise) = 0.175
      double MOVE4 = 0.675; //p(90 degrees clkwise) = 0.125
      double MOVE5 = 0.8; //p(90 degrees counterclkwise) = 0.125
      double MOVE6 = 0.875; //p(135 degrees clkwise) = 0.075
      double MOVE7 = 0.95; // p(135 degrees counterclkwise) = 0.075
      double MOVE8 = 1.0; //p(180 degrees) = 0.05
      double LAY = 0.23; // the prob of a butterfly ovipositing upon
      //landing.

      Frustration = 0;

      int location = 0; //location is where the butterfly is.
      //int fly = 1; // f counts the number of adults
      for (int fly=0;fly<dailylog[day].adults;fly++)
      {
            double r = ((double) RandomInteger/RIMAX);
            location = ((int) floor (r * Totalplants)); //Starts the
            //Butterfly at a random plant
            //each butterfly has a movement bias:
            double r6 = ((double) RandomInteger/RIMAX);
            int directcase = (int)ceil(r6 * 4); // directcase randomly
            //assigns which of four potential biases the butterfly will
            //fly towards (N - case 2, S - case 3, E - case 1, W - case
            // 4).
            int direction1 = 0; // the primary direction
            int direction2 = 0;
            int direction3 = 0;
            int direction4 = 0;
      // If the direction1 = 1, the butterfly is biased to move
      //right across the field
      // If the direction1 = -1, the butterfly is biased to move left
      // If the direction1 = 20, the butterfly is biased to move down
      // If the direction1 = -20, the butterfly is biased to move up.
            switch(directcase)
            {
            case 1:
```

```
                direction1 = 1;
                direction2 = Rowsize;
                direction3 = -1;
                direction4 = -Rowsize;
                break;
        case 2:
                direction1 = Rowsize;
                direction2 = -1;
                direction3 = -Rowsize;
                direction4 = 1;
                break;
        case 3:
                direction1 = -1;
                direction2 = -Rowsize;
                direction3 = 1;
                direction4 = Rowsize;
                break;
        case 4:
                direction1 = -Rowsize;
                direction2 = 1;
                direction3 = Rowsize;
                direction4 = -1;
                break;
} //ends the butterfly bias

int egg = 0;
do {
        double r = ((double) RandomInteger/RIMAX);
        if (r <= ZERO) // if butterfly doesn't move for a timestep:
        {
                location = location;
        }
        else // if butterfly moves:
        {
                double r2 = ((double) RandomInteger/RIMAX);
                if (r2 <= MOVE1) location = location + direction1;
                //move to primary bias
                if (MOVE1 < r2 && r2 <= MOVE2) location = location +
                direction1 + direction2;//move to next bias
                if (MOVE2 < r2 && r2 <= MOVE3) location = location +
                direction1 + direction4; //move to next bias
                if (MOVE3 < r2 && r2 <= MOVE4) location = location +
                direction2; // move to next bias
                if (MOVE4 < r2 && r2 <= MOVE5) location = location +
                direction4; // move to next bias
                if (MOVE5 < r2 && r2 <= MOVE6) location = location +
                direction3 + direction2; // move to next bias
                if (MOVE6 < r2 && r2 <= MOVE7) location = location +
                direction3 + direction4;
                if (MOVE7 < r2 && r2 <= MOVE8) location = location +
                direction3;

                if (location >= Totalplants) location = location -
                Totalplants;
                if (location < 0) location = location + Totalplants;
```

```
      // Note- using this method, there's no way to prevent a butterfly
      //from wrapping around a border. So, if it was on the last plant of
      //a row, and moved one more, it would be on the first plant of the
      // next row.
      }
      double r4 = ((double) RandomInteger/RIMAX);
      if (r4 <= LAY) // It does not oviposit on every plant it stops at.
      {
            int k = -1;
            do k++; while((plant[location].herbivore[k]>0)&&(k<20));
            // looks for the first empty spot
            if ((plant[location].herbivore[k]==0)&&(k<20))
            {
                  plant[location].herbivore[k] = 1;
                  egg++;
            }
            if (k == 20) Frustration++;
            if (Frustration > 10) egg = Oviposition;
      } // ends lay loop
} while (egg < Oviposition);//ends single butterfly egglaying
//fly++;
} //while (fly <= dailylog[day].adults);// ends single butterfly
//ovipositing + initialization
//NOTE = SET dailylog[day].adults to 1 FOR DEBUGGING PURPOSES ABOVE

//INDUCTION ROUTINE:
      for (int n=0; n < Totalplants; n++)
      {
            plant[n].induction=0; // Assume the basal state is off
            bool bigchew=0; // Switch for whether an old enough
            //caterpillar is on
            for (int p=0; p < 20; p++)
            {
            if (plant[n].herbivore[p]>=(6+Induction) &&
                  plant[n].herbivore[p] <= 21) bigchew=1;//pupae don't eat
            }
            if (bigchew) // so, if the plant has a big caterpillar...
            {
                  plant[n].induction=1;//The plant turns on
                  plant[n].relaxdelay=1;//and the plant timer is kept at 1
            }
            if (!bigchew) // If there isn't a big caterpillar...
            {
                  if (plant[n].relaxdelay > Relaxation) // if the plant
                  //has used up the timer..
                  {
                     plant[n].induction=0; //... induction stays off
                     plant[n].relaxdelay=0;// and timer sent to 0.
                  }
                  if (plant[n].relaxdelay > 0) //if the plant has not used
                  //up timer... (took out && anylarvae == 0)
                  {
                     plant[n].induction=1; //Plant goes on
                     plant[n].relaxdelay++;//and the timer is added on to.
                  }
```

```
            }// ends empty plant options

      }//end induction


// PARASITOID FORAGING:
if(fifthday == 0)
{
      wasptime = 0; //timer for the waps
      double r = ((double) RandomInteger/RIMAX);
      wasplocation = ((int) floor (r * Totalplants)); //Starts the
      //wasp at a random plant
      list <int> PlantsVisited; // keeps track of all the plants
      //visited
      FlyBias[0] = 25; //bias for 1 meter
      FlyBias[1] = 13; //bias for 2 meters
      FlyBias[2] = 3; // bias for 3 meters
      FlyBias[3] = 2; // bias for 4 meters
      FlyBias[4] = 1; // bias for 4 meters
      TotalAvailPlants = FlyBias[0]*4 + FlyBias[1]*8 + FlyBias[2]*12
            + FlyBias[3]*16 + FlyBias[4]*20; //size of bias array
      WaspPath[0] = wasplocation;
      Visitcounter = 1;

      do
      {
            PlantsVisited.push_back(wasplocation);
            WaspPath[Visitcounter] = wasplocation;

            //Does plant have any unparasitized larvae?
            bool gottago = 0; // if gottago is true, the wasp will leave
            //the plant its on before checking every herbivore spot.
            for (int k = 0; k < 20; k++)
            {
                  if (!gottago)
                  {// Its timer hasn't run out on the plant
                  if ((plant[wasplocation].herbivore[k] >= 6) &&
                        (plant[wasplocation].herbivore[k] <= Attack) &&
                        (plant[wasplocation].parasitism[k] == 0))
                  { //It scores a sting!
                        wasptime += (Giveup * 0.5);
                        plant[wasplocation].parasitism[k] = 1;
                        wasptime += HandleTime;
                        dailylog[day].waspeggs++;
                        double r9 = ((double) RandomInteger/RIMAX);
                        if (r9 > 0.33) gottago = 1; //chooses to leave
                        //after 33% of all stings
                  }
                  if ((k == 19) && ((plant[wasplocation].herbivore[k] <
                        6)|| plant[wasplocation].herbivore[k] > Attack ||
                        plant[wasplocation].parasitism[k] != 0))
                  {// It doesn't score a sting...
                        wasptime += Giveup;
                  }
                  }// ends if(gottago)
```

```
      }// ends within-plant searching

      nextavail = 0;
      //Creates the Picking List:
      for (int xdistance = -5; xdistance <= 5; xdistance++)
      {
         for (int ydistance = -5; ydistance <= 5; ydistance++)
         {
            WaspDistance = abs(xdistance) + abs(ydistance);
            if (WaspDistance <= 5 && WaspDistance > 0)
            {
               targetplant = wasplocation + xdistance + ydistance
                  * Rowsize;
               if (targetplant < 0) targetplant = targetplant +
               Totalplants; //wrap under
               if (targetplant >= Totalplants) targetplant =
                  targetplant - Totalplants; // wrap over
               for (int h = 0; h < FlyBias[WaspDistance - 1]; h++)
               {
                  AvailablePlants[nextavail] = targetplant; //adds
                  //to random list
                  if (plant[targetplant].induction != 0)
                        AvailableSignal[nextavail] = targetplant;
                        //if induced, adds to signal list
                  else AvailableSignal[nextavail] = Totalplants + 1;
                  // if not induced, adds 401
                  if (targetplant == WaspPath[Visitcounter - 1])
                  //checks if it was the plant the wasp came from
                  {
                        AvailablePlants[nextavail] = Totalplants+1;
                        //if so, adds 401
                        AvailableSignal[nextavail] = Totalplants+1;
                        // if so, adds 401
                  }
                  nextavail++;
               }//ends loop placement
            }//end wasp distance checker
         } // end row counter
      } // end column counter

//Checks for any signaling plants in range:
      bool SignalCheck = 0;
      for (int l = 0; l < TotalAvailPlants; l++) if
            (AvailableSignal[l] < Totalplants) SignalCheck = 1;

//Moves the wasp:
      NextPlant = 0;
      do
      {
            double r2 = ((double) RandomInteger/RIMAX);
            Picker = r2 * TotalAvailPlants;
            if (RBRandom ->Checked)
            {
              if (AvailablePlants[Picker] < Totalplants)
              {
```

```
                  wasplocation = AvailablePlants[Picker];
                  NextPlant = 1;
               }
            }
            if (RBSignal -> Checked)
            {
               if (!SignalCheck)
               {
                  if (AvailablePlants[Picker] < Totalplants)
                  {
                        wasplocation = AvailablePlants[Picker];
                        NextPlant = 1;
                  }
               }
               else
               {
                  if(AvailableSignal[Picker] < Totalplants)
                  {
                        wasplocation = AvailableSignal[Picker];
                        NextPlant = 1;
                  }//ends plant check
                }//ends else
             }// ends signal button
      }while(!NextPlant); //NextPlant will be false if the picker
      //chooses a plant that's Total+1

      PreviousPlant = WaspPath[Visitcounter];
      Visitcounter++;
      xdist = abs(plant[wasplocation].column -
            plant[PreviousPlant].column);
      ydist = abs(plant[wasplocation].row -
            plant[PreviousPlant].row);
      if (xdist > 5) xdist = Rowsize - xdist; //account for
      //wraparound
      if (ydist > 5) ydist = Rowsize - ydist; //account for
      //wraparound
      WaspDistance = sqrt((double) xdist*xdist + ydist*ydist);
      wasptime += WaspDistance * Flight; //need to add travel time
      //to the wasp's time spent
}while (wasptime < TIME); // Ends Parasitoid Foraging

// Prints out where the wasp went on day 10:
/*     if (day == 10)
      {
            fprintf(Output6, "%s \n", "Day 10 Path");
            list <int>::iterator PV_Iter;
            for ( PV_Iter = PlantsVisited.begin( ); PV_Iter !=
            PlantsVisited.end( ); PV_Iter++ )
            fprintf(Output6," %d \n", *PV_Iter);
      }
*/

// Finds out how many plants the wasp actually visited:
PlantsVisited.sort();
PlantsVisited.unique();
```

```
      dailylog[day].plantsvisited = PlantsVisited.size();
      //fprintf(Output6,"%s %d \n", "Unique plants visited: ",
      //dailylog[day].plantsvisited);
      fprintf(Output6,"%d %d %d \n", day, dailylog[day].plantsvisited,
            dailylog[day].waspeggs);

}// end Wasp Foraging Section


// RECKONING OF PLANT STATE:
      int sum = 0; // sum adds up the number of larvae in the parasitoid's
      //attack range
      NO = 0;
      SO = 0;
      SE = 0;
      NE = 0;
      int isinduced=0; //counts up the number of induced plants
      for (int h = 0; h < Totalplants; h++)
      {
            if(fifthday == 0) fprintf(Output2,"%d ", h);
            bool larvaeYN = 0;
            bool inductYN = 0;
            for (int j = 0; j < 20; j++)
            {
                  //fprintf(Output2, "%d ", plant[h].herbivore[j]);
                  // prints out the larva
                  //fprintf(Output2, "%d ", plant[h].parasitism[j]);
                  // prints out parasitism state
               if ((plant[h].herbivore[j] > 0) && (plant[h].herbivore[j]
                  <=5)) dailylog[day].eggs++;
               if ((plant[h].herbivore[j] >= 6) && (plant[h].herbivore[j]
                  <=8))
               {
                  dailylog[day].firsts++;
                  if (plant[h].parasitism[j] != 0)dailylog[day].pfirsts++;
               }
               if ((plant[h].herbivore[j] >= 9) && (plant[h].herbivore[j]
                  <=11))
               {
                  dailylog[day].seconds++;
                  if (plant[h].parasitism[j] != 0)
                  dailylog[day].pseconds++;
               }
               if ((plant[h].herbivore[j] >= 12) && (plant[h].herbivore[j]
                  <=14))
               {
                  dailylog[day].thirds++;
                  if (plant[h].parasitism[j] != 0)dailylog[day].pthirds++;
               }
               if ((plant[h].herbivore[j] >= 15) && (plant[h].herbivore[j]
                  <=17))
               {
                  dailylog[day].fourths++;
                  if (plant[h].parasitism[j] != 0)
                        dailylog[day].pfourths++;
```

```
                }
                if ((plant[h].herbivore[j] >= 18) && (plant[h].herbivore[j]
                   <=20))
                {
                   dailylog[day].fifths++;
                   if (plant[h].parasitism[j] != 0)dailylog[day].pfifths++;
                }
                if ((plant[h].herbivore[j] >= 21) && (plant[h].herbivore[j]
                   <=28))
                {
                   dailylog[day].pupae++;
                }
                if ((plant[h].herbivore[j] >= 6) && (plant[h].herbivore[j]
                   <= Attack))//Only viable instars targets
                {
                   sum += 1;
                   larvaeYN = 1; // If a viable instar is present the plant
                   //is credited as occupied
                }
             } // end occupation check
             if (plant[h].induction !=0)
             {
                   inductYN = 1; //signaling check
                   isinduced++;
             }
             if (larvaeYN == 1 && inductYN == 0)
             {
                   NO += 1; // plants occupied, but not signalling
                   if(fifthday == 0) fprintf(Output2, "%s \n", "NO");
             }
             if (larvaeYN == 1 && inductYN == 1)
             {
                   SO += 1; // plants occupied and signalling
                   if(fifthday == 0) fprintf(Output2, "%s \n", "SO");
             }
             if (larvaeYN == 0 && inductYN == 1)
             {
                   SE += 1; // plants empty and signalling
                   if(fifthday == 0) fprintf(Output2, "%s \n", "SE");
             }
             if (larvaeYN == 0 && inductYN == 0)
             {
                   NE += 1; // plants empty, but not signalling
                   if(fifthday == 0) fprintf(Output2, "%s \n", "NE");
             }
      }//end plant totals

fprintf(Output4," %d %d %d %d %d %d %d %d %d %d %d %d %d \n",
      dailylog[day].eggs, dailylog[day].firsts, dailylog[day].pfirsts,
      dailylog[day].seconds, dailylog[day].pseconds, dailylog[day].thirds,
      dailylog[day].pthirds, dailylog[day].fourths,
      dailylog[day].pfourths, dailylog[day].fifths,
      dailylog[day].pfifths, dailylog[day].pupae, dailylog[day].adults);
if(fifthday == 0) fprintf(Output3, "%d %d %d %d %d \n", day, NO, SO, SE,
      NE);
```

```
}// <- END DAY HERE
//////////////////////////////////////////////////////////
// RECKONING OF PLANT STATE:
      int sum = 0; // sum adds up the number of larvae in the parasitoid's
      //attack range
      NO = 0;
      SO = 0;
      SE = 0;
      NE = 0;
      for (int h = 0; h < Totalplants; h++)
      {
            if(fifthday == 0) fprintf(Output2," %d %d %s ", h,
            plant[h].induction, " : "); // prints induction state
            bool larvaeYN = 0;
            bool inductYN = 0;
            for (int j = 0; j < 20; j++)
            {
               if(plant[h].herbivore[j] >= 6 && plant[h].herbivore[j] <=
                  Attack)//Only viable instars targets
               {
                  sum += 1;
                  larvaeYN = 1; // If a viable instar is present the plant
                  //is credited as occupied
               }
               if (plant[h].induction !=0) inductYN = 1;
               //fprintf(Output2, "%d ", plant[h].herbivore[j]);
               // prints a list for each herbi spot.
            }
               //fprintf(Output2, " %d ", sum);
            if (larvaeYN == 1 && inductYN == 0)
            {
                  NO += 1; // plants occupied, but not signalling
                  if(fifthday == 0) fprintf(Output2, "%s \n", "NO");
            }
                  if (larvaeYN == 1 && inductYN == 1)
                  {
                        SO += 1; // plants occupied and signalling
                        if(fifthday == 0) fprintf(Output2, "%s \n", "SO");
                  }
                  if (larvaeYN == 0 && inductYN == 1)
                  {
                        SE += 1; // plants empty and signalling
                        if(fifthday == 0) fprintf(Output2, "%s \n", "SE");
                  }
                  if (larvaeYN == 0 && inductYN == 0)
                  {
                        NE += 1; // plants empty, but not signalling
                        if(fifthday == 0) fprintf(Output2, "%s \n", "NE");
                  }
            }


// SPATIAL AUTOCORRELATION STATISTICS:
```

```
// Initialize statistics variables:
long long rstat = 0, Snot = 0, Winot = 0, Wnoti = 0, Sone = 0, Stwo = 0;
long long Tnot = 0, Yinot = 0, Ynoti = 0, Tone = 0, Ttwo = 0;
long long ntwo = 0, nthree = 0, nfour = 0;
double Expr = 0, varr = 0, zstat = 0;
double varr1 = 0, varr2 = 0, varr3 = 0, varr4 = 0;
bool Wij[400][400], Yij[400][400];
for (int a = 0; a < 400; a++)
{
      for (int b = 0; b < 400; b++)
      {
            Wij[a][b] = 0;
            Yij[a][b] = 0;
      }
}

// plant[m].occupied is the flag for the "black/white" measure of the
//stats.
for(int m = 0; m < Totalplants; m++)
{
      for(int n = 0; n < 20; n++)
      {
            if(plant[m].herbivore[n] >= 6 && plant[m].herbivore[n] <= 20)
            plant[m].occupied = 1;
      }
}

// Create the W matrix of spatial proximity:
for (int i = 0; i < Totalplants; i++)
{
      for (int j = 0; j < Totalplants; j++)
      {
            if((abs(plant[i].row-plant[j].row) == 1) && (plant[i].column-
                  plant[j].column == 0)) Wij[i][j] = 1;
            if((plant[i].row-plant[j].row == 0) && (abs(plant[i].column-
                  plant[j].column) == 1)) Wij[i][j] = 1;
      }
}// ends building the W matrix

//fprintf(Output5, "%s \n", "Proximity matrix (Wij): ");
//for (int b = 0; b < Totalplants; b++)
//{
//    for (int c = 0; c < Totalplants; c++) fprintf(Output5," %d ",
//    Wij[b][c]);
//    fprintf(Output5 ,"%s \n"," ");
//}

// Create the Y matrix of Values (0 = BB or WW, 1 = BW)
for (int i = 0; i < Totalplants; i++)
{
      for (int j = 0; j < Totalplants; j++)
      {
            if (plant[i].occupied != plant[j].occupied) Yij[i][j] = 1;
      }
}// ends building the Y matrix
```

```
//fprintf(Output5, "%s \n", "Value matrix (Yij): ");
//for (int b = 0; b < Totalplants; b++)
//{
//    for (int c=0; c < Totalplants; c++) fprintf (Output5," %d ",
//Yij[b][c]);
//    fprintf(Output5, "%s \n", " ");
//}

// Other calculations...
for (int m = 0; m < Totalplants; m++)
{
      for (int n = 0; n < Totalplants; n++)
      {
            rstat = rstat + (Wij[m][n] * Yij[m][n]);
            if (m != n) Snot = Snot + Wij[m][n];
            if (m != n) Sone = Sone + ((Wij[m][n] + Wij[n][m]) *
                  (Wij[m][n] + Wij[n][m]));
            Winot = Winot + Wij[m][n];
            Wnoti = Wnoti + Wij[n][m];
            if (m != n) Tnot = Tnot + Yij[m][n];
            if (m != n) Tone = Tone + ((Yij[m][n] + Yij[n][m]) *
                  (Yij[m][n] + Yij[n][m]));
            Yinot = Yinot + Yij[m][n];
            Ynoti = Ynoti + Yij[n][m];
      }// ends n loop
      Stwo = Stwo + ((Winot + Wnoti) * (Winot + Wnoti));
      Ttwo = Ttwo + ((Yinot + Ynoti) * (Yinot + Ynoti));
      Winot = 0; Wnoti = 0; Yinot = 0; Ynoti = 0;
}// ends m loop
Sone = Sone / 2;
Tone = Tone / 2;
ntwo = Totalplants * (Totalplants - 1);
nthree = ntwo * (Totalplants - 2);
nfour = nthree * (Totalplants - 3);
Expr = (double) Snot * Tnot / ntwo;
varr1 = (double) (Sone*Tone) / (2*ntwo);
varr2 = (double) (Stwo - 2*Sone) * (Ttwo - 2*Tone) / (4*nthree);
varr3 = (double) (Snot*Snot + Sone - Stwo) * (Tnot*Tnot + Tone - Ttwo) /
      nfour;
varr4 = Expr * Expr;
varr = varr1 + varr2 + varr3 - varr4;
zstat =(abs(rstat - Expr)- 1)/ sqrt(varr);
fprintf(Output5, " %s %d \n", "The r value is: ", rstat);
fprintf(Output5, " %s %f \n", "The expected r is: ", Expr);
fprintf(Output5, " %s %f \n", "The variance is: ", varr);
fprintf(Output5, " %s %f \n", "The z statistic is: ", zstat);
//END STATISTICS ROUTINE

      fclose(Output4);
      fclose(Output2);
      }// END for MULTIPLE RUNS

fclose(Output3);
```

```
fclose(Output5);
fclose(Output6);
system("PAUSE");
}//END START BUTTON


};
}
```

A3. Growers Survey of Environmental Best Management Practices

Part I. Current Practices:

Which of the following practices have you used in the past two years?

_____ 1. Scout your fields for insects, weeds, and diseases

_____ 2. Use economic thresholds to determine when to apply insecticides for insect control

_____ 3. Use economic thresholds to determine when to apply herbicides for weed control

_____ 4. Select insecticides, fungicides, and herbicides that have low environmental impacts

_____ 5. Crop rotation

_____ 6. Rotate the mode of action or use multiple modes of action for herbicides

_____ 7. Rotate the mode of action or use multiple modes of actions for insecticides

_____ 8. Plant cover crops

_____ 9. Plant buffer zones

_____ 10. Select seeds based on drought tolerance or disease resistance.

_____ 11. Use biological control to reduce insects, weeds, and diseases

_____ 12. Use reduced-till, no-till, or conservation tillage

_____ 13. Time your plantings to minimize the chance of pest outbreaks

_____ 14. Selectively apply pesticides in "hotspots" as opposed to blanket applications

_____ 15. Sample your soil for nutrients to fertilize to the extent needed

_____ 16. Contact the extension service for advice about a specific IPM problem

_____ 17. Hire a consultant that has been trained in Integrated Pest Management

_____ 18. Use calendar-based spraying for insects other than thrips*

Part II. Technology

Please indicate if you use the following technology in your operations, and if not, why not?

_____ 19. Genetically-modified seeds (e.g. Bt, Round-up ready) _____

_____ 20. Beneficials' habitat mixes (e.g. wildflower border)_____

_____ 21. Augmented biological control (e.g. ladybug releases) _____

_____ 22. Pest monitoring traps (blacklight, pheromone) _____

_____ 23. IPM compatible insecticides _____

_____ 24. Control drainage/water control structures_____

_____ 25. Drip (Low-pressure) irrigation _____

_____ 26. Weather monitoring/forecasting systems _____

_____ 27. Online IPM information_____

_____ 28. GPS for precision agriculture _____

Part III. Attitudes towards Integrated Pest Management (IPM)

IPM is the combined use of chemical, biological, and cultural controls to limit insects, weeds, and diseases in a manner that minimizes risk to humans and the environment. How strongly do you agree with the following statements regarding IPM? Do you *Strongly Agree*, *Somewhat Agree*, *Neither Agree nor Disagree*, *Somewhat Disagree*, or *Strongly Disagree* with the statement?

Statement	Strongly Agree	Somewhat Agree	Neither Agree nor Disagree	Somewhat Disagree	Strongly Disagree
29. I believe that IPM does **not** provide any advantages to my farm.	-2	-1	0	1	2
30. I feel that cotton produced with IPM is of equal quality with conventionally produced cotton.	2	1	0	-1	-2
31. I believe that conventional production is **no** worse for the environment than any other production method.	-2	1	0	1	2
32. I believe that IPM reduces chemical residue in the water supply.	2	1	0	-1	-2
33. I think that corporate buyers are interested in IPM grown products.	2	1	0	-1	-2
34. I feel that using IPM puts me at a disadvantage for selling my crop.	-2	-1	0	1	2
35. I believe that the NC Cotton Producers Assoc. endorses IPM.	2	1	0	-1	-2
36. I feel that my customers would be interested in IPM.	2	1	0	-1	-2
37. I believe that most growers with farm operations similar to mine do **not** implement IPM.	-2	-1	0	1	2
38. I think that there is **no** market advantage for growing IPM cotton.	-2	-1	0	1	2
39. I do **not** think that local growers favor IPM.	-2	-1	0	1	2
40. I feel that my competitors are increasingly using IPM.	2	1	0	-1	-2
41. I believe that my county extension agent can answer my questions about IPM.	2	1	0	-1	-2
42. I trust the information I get from private crop consultants.	-2	-1	0	1	2
43. I think that the internet is helpful for getting information on IPM, specific to my crops.	2	1	0	-1	-2
44. I think that the state extension service does not provide growers with enough information about IPM.	-2	-1	0	1	2

Part IV. Potential IPM Policies

I am going to describe several hypothetical policies that the government could enact to encourage growers' use of IPM. I would like you to say whether you *Strongly Agree, Somewhat Agree, Neither Agree nor Disagree, Somewhat Disagree,* or *Strongly Disagree* with the policy, and then explain your reasoning.

45. The government should create a certification and branding program. For this program, you would decide if you want your farm to be inspected for IPM practices, and if you met the requirements, you would be able to use the government label on your products.

STRONGLY AGREE	SOMEWHAT AGREE	NEITHER AGREE NOR DISAGREE	SOMEWHAT DISAGREE	STRONGLY DISAGREE

Explain:

_____

_____

46. The government should create a program to reduce the economic risks of using IPM. At the beginning of the season, if you volunteered for the proposed program, you would plant the majority of your field according to strict guidelines, as well as a test strip that you would treat normally. At the end of the season, government representatives would determine if you had a reduction in yield due to the IPM practices, and pay you the difference if you had a reduction in yield.

STRONGLY AGREE	SOMEWHAT AGREE	NEITHER AGREE NOR DISAGREE	SOMEWHAT DISAGREE	STRONGLY DISAGREE

Explain:

_____

_____

47. The government should increase the extension service's budget to provide for more agent-led programs in IPM practices. County agents should have more resources for demonstrating how to implement best management practices on local farms.

STRONGLY AGREE	SOMEWHAT AGREE	NEITHER AGREE NOR DISAGREE	SOMEWHAT DISAGREE	STRONGLY DISAGREE

Explain:

_____

_____

48. The government should provide financial assistance for growers wishing to purchase expensive technology used in IPM, such as weather monitoring stations. This financial assistance would come in the form of a tax credit or reduced rate loan.

STRONGLY AGREE	SOMEWHAT AGREE	NEITHER AGREE NOR DISAGREE	SOMEWHAT DISAGREE	STRONGLY DISAGREE

Explain (are there some technologies you think this would be more or less appropriate for?):

_____

_____

49. The government should more tightly regulate the costs of pesticides based on their environmental effects, such that those deemed to have minimal impact would be less expensive for you to purchase.

STRONGLY AGREE	SOMEWHAT AGREE	NEITHER AGREE NOR DISAGREE	SOMEWHAT DISAGREE	STRONGLY DISAGREE

Explain:

_____

_____

50. The government should invest more money in scientific research that is directly applicable to developing IPM practices that can be used in cotton production.

STRONGLY AGREE	SOMEWHAT AGREE	NEITHER AGREE NOR DISAGREE	SOMEWHAT DISAGREE	STRONGLY DISAGREE

Explain (What kind of agricultural research projects should the government fund?):

_____

_____

51. The government should be more active in regulating compliance with resistance management refuge requirements. Growers who do not plant the recommended refuge for pest resistance management should be held accountable.

STRONGLY AGREE	SOMEWHAT AGREE	NEITHER AGREE NOR DISAGREE	SOMEWHAT DISAGREE	STRONGLY DISAGREE

Explain (What proportion of your fields is a treated refuge? How else could resistance be managed?):_____

_____

Part V. Potential Water Quality Practices

52. If you were to implement water quality buffers, what would you consider an acceptable width and what management flexibility would you need to have (e.g. height of vegetation, mowing, type of vegetation, access)?

53. Under what conditions would you be willing to set aside land for a conservation easement if you were reimbursed for the loss of land? How long would you be willing to set aside land (10 years, permanently...)?

54. What kinds of problems have you had with your current drainage system, and what have you tried to do to improve the situation?

55. Would you be willing to participate in a watershed credits trading program, such that if you reduced your chemical inputs you could sell these credits to others but would have to buy credits if you increased your chemical inputs?

Part VI. Demographics

56. How many years have you been involved in farm management? _____

57. What crops did you grow last year? About how many acres of did you have of each crop this last year?

Other Crops	**2005 Acres**
_____	_____
_____	_____

58. What percent of your family's total gross income comes from non-farm sources?

_____ **% non-farm**

59. Which of the following best describes your education. **[Read choices]**:

(__) – Some high school
(__) – High school graduate
(__) – Some college
(__) – College graduate
(__) – Some graduate school
(__) – A Post-graduate degree

60. Which of the following best describes you:

(__) You are among the first one-third of growers in your area to try and adopt a new product or farming practice

(__) You are among the middle one-third of growers in your area to try and adopt a new product or farming practice

(__) You are among the last one-third of growers in your area to try and adopt a new product or farming practice

61. Do you belong to any conservation organizations? Yes (__) No (__)

62. In what year were you born? _____ **Year**

63. Would you be willing to tell me which range your gross farm income was in?

1 = $0 –$30,999
2 = $40,000 - $99,999
3 = $100,000 - $249,999
4 = $250,000 – $499,999
5 = $500,001 – $999,999
6 = $1,000,000+
7 = Don't know
8 = Refused

Thank you for participating in this survey. I appreciate your time. If you have any questions, please feel free to contact me using the information on the informed consent form.