

What omnivores eat: direct effects of induced plant resistance on herbivores and indirect consequences for diet selection by omnivores

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Summary

1. Omnivory, where an animal crosses trophic boundaries, is thought to be common in natural and managed communities. Foraging theory predicts that omnivores will balance their diet as a result of nutritional needs, food quality and availability of alternate foods. We investigated diet selection of the western flower thrips [*Frankliniella occidentalis* (Pergande)], a herbivore under some circumstances, and a predator under other circumstances.

2. We demonstrate that induced plant resistance can indirectly affect diet selection by thrips. The density of herbivorous spider mites is reduced on induced plants compared to controls and is also positively correlated with the number of mite eggs that the thrips consume.

3. In choice tests, mite eggs from induced plants were less preferred by thrips than eggs from control plants. Mite egg size was also smaller on induced plants compared to controls. However, this alone did not explain the diet selection by thrips. In a field experiment, thrips avoided colonizing induced plants, but they were attracted to induced plants that we inoculated with mites. Thus, the presence of herbivorous prey on induced plants attenuated the negative effects of induced resistance on thrips colonization.

4. Feeding decisions of thrips can be influenced by several factors. We showed previously (Agrawal, Kobayashi & Thaler 1999a) Influence of prey availability and induced host plant resistance on omnivory by western flower thrips. (*Ecology*, **80**, 518–523.) that reducing plant quality can cause omnivores to shift towards relatively more predation than herbivory. We show now that on induced plants, reduced prey density and quality may antagonize this shift towards increased predation.

5. Induced plant resistance has negative effects on both the plant-based food resource (direct effect) and the animal-based food resource (indirect effect) of omnivorous thrips. Thus, variation in the quantity and quality of food items interact to determine the diet selection of omnivores.

Key-words: herbivory, induced plant resistance, omnivory, optimal diet selection, tritrophic interactions.

Journal of Animal Ecology (2000) **69**, 525–535

Introduction

Omnivores are animals that feed on more than one trophic level (e.g. animals and plants). Predicting diet selection in omnivores is a complex mix of

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understanding foraging strategies, nutritional requirements, and the availability of foods (Schoener 1971; Westoby 1978). For several reasons, diet selection in omnivores may be more complicated than in non-omnivores; for example, different prey have extremely divergent antipredator strategies (e.g. fleeing behaviour in animals and chemical defences of plants). Omnivores may forage on foods even when these can only sustain their survival (e.g. nectar and phloem) and not reproduction. Thus, various factors including the availability, nutritional quality, and defensive strategy of plants and animals may influence an omnivore's diet selection.

It is important to understand the complexities of diet selection in omnivores because they are integral species in most natural communities (Polis, Myers & Holt 1989; Polis 1991; Polis & Strong 1996; Polis & Winemiller 1996). In addition, omnivores that feed on animals and plants are ever-present in agroecosystems, where they can be beneficial through their consumption of herbivores, or detrimental through their consumption of crops (Rosenheim *et al.* 1995; Alomar & Wiedenmann 1996; Agrawal & Karban 1997; Coll & Ruberson 1998). The focus of this study was to understand how variation in plant quality directly and indirectly influenced diet selection in an omnivore commonly found in natural and agricultural ecosystems.

Many biotic and abiotic factors can influence the quality of food items for omnivores; for example, any factor that influences the health or size of prey may affect the value of that prey to an omnivore. In addition, both plants and animals have inducible defence systems in which non-lethal exposure to a parasite or predator can induce defences in the host organism (Tollrian & Harvell 1998). Such induced defences include behavioural (e.g. Winkler 1994), morphological (McCollum & Van Buskirk 1996; Agrawal 1998a, 1999), and chemical defences (Karbon & Baldwin 1997; Agrawal, Tuzun & Bent 1999b), as well as the recruitment of biotic defenders (e.g. ants, predators and parasitoids) (Agrawal 1998b; Agrawal & Rutter 1998; Sabelis *et al.* 1999). Thus, phenotypic variation within a species could present omnivores with foods of alternate value. Two recent studies have shown that changes in intraspecific food quality of plants can cause profound shifts in the diet choices of omnivores (Agrawal, Kobayashi & Thaler 1999a; Eubanks & Denno 1999).

As plant quality decreases, the relative benefits of consuming alternative foods should increase. Plant quality, however, may also indirectly affect omnivory and its effect on herbivorous prey. For example, plant resistance traits often reduce herbivore population size (Karbon 1992), make individual herbivores smaller (Karbon & Baldwin 1997), and change the chemical defences of herbivores themselves (Duffey 1980) compared to herbivores on less resistant

plants. If prey density, size, and quality affect the feeding decisions of omnivores, then plant resistance may have mixed effects on omnivores. It was previously shown in this system that induced plant resistance caused omnivores to reduce herbivory and increase carnivory (Agrawal *et al.* 1999a). Plant resistance traits may lower prey quantity and quality and thereby antagonize an omnivore's tendency to become more predatory in the face of increased plant resistance.

In this study, we investigated how induced resistance of cotton plants affects herbivorous spider mites and how this indirectly affects feeding decisions of the omnivorous western flower thrips [*Frankliniella occidentalis* (Pergande)]. Specifically, we asked: (i) what is the effect of prey density on consumption of plants vs. prey? (ii) are there indirect effects of induced resistance on thrips mediated through changes in prey quality? (iii) are the changes in prey quality explained by changes in prey size? and (iv) how do induced plant resistance and prey availability affect plant colonization by thrips?

Materials and methods

STUDY SYSTEM

Frankliniella occidentalis has been a model organism for studying omnivory. The thrips feed on pollen, small arthropods and leaf cell contents. It is a cosmopolitan species of worldwide economic importance. *Frankliniella occidentalis* has a short generation time (≈ 10 days) and is a major pest species of many agricultural crops (Parker, Skinner & Lewis 1995) and wild plants (A. Agrawal, personal observation). Alternatively, *F. occidentalis* and other omnivores in the cotton agroecosystem are predators of spider mite eggs, and can increase plant reproductive yield compared to plants with fewer omnivores (Wilson, Trichilo & Gonzalez 1991; Agrawal & Karban 1997; Agrawal, Karban & Colfer 2000). Several aspects of omnivory, including diet mixing (Trichilo & Leigh 1988), diet selection (Agrawal *et al.* 1999a), chemical ecology (Teering 1995; Pallini, Janssen & Sabelis 1997, 1999), and species interactions in the field (Trichilo & Leigh 1986b; Agrawal & Karban 1997; Agrawal *et al.* 2000) have been well studied in *F. occidentalis*. Our continuing goal is to study the complexities of food choice in this omnivore and to develop an understanding of how to manipulate omnivores to be less severe pests and better biological control agents.

GENERAL PROCEDURES

Cotton plants (*Gossypium hirsutum* L. var. Acala SJ-2) were grown in 125 mL pots in greenhouse soil (UC Mix, Redi Gro, Inc., Sacramento, California, USA) in a growth chamber maintained at 27 °C

with a 16:8 light:dark (L:D) cycle. Thrips were obtained from a colony maintained on beans; prey (spider mite eggs) were obtained from a colony of *Tetranychus pacificus* McGregor maintained on cotton seedlings. Spider mite eggs were collected using methods described in detail by Scriven & McMurtry (1971). Briefly, infested cotton seedlings were put in a water bath with a few drops of bleach to dissolve the mite webbing and release the mites into suspension. The water was then passed through a series of four mesh-lined containers. The mesh size sequentially decreased to catch unwanted debris, adult female mites, immature and male mites, and eggs, respectively. Eggs were transferred from the container and collected on filter paper by using a Buchner funnel. Thrips and spider mite eggs were transferred for experiments using a fine paintbrush.

EFFECTS OF PREY DENSITY ON OMNIVORY

The first experiment was designed to test for the effects of prey density on the relative amounts of plant feeding and predation by thrips. Given that induced resistance of cotton plants reduces the density of spider mite prey (Karban & Carey 1984; Karban 1987), this experiment examined a potential indirect effect of induced resistance on omnivory. Spider mite eggs were placed on a single, excised cotton cotyledon (undamaged) on moistened filter paper in a 90-mm diameter Petri dish at densities of 0, 5, 10, 15, 20 and 25 mite eggs per leaf. These levels represent the range of mite densities commonly found in the field (Agrawal *et al.* 2000). A single thrips was then introduced and the dish was sealed with parafilm. After 4 days (the leaves remained turgid), the number of mite eggs consumed and the number of feeding scars on each plant were counted with the help of a dissecting microscope. Mite eggs rarely hatched during this period, and if they did, the replicate was discarded. Feeding scars on the leaves were discrete pits created by thrips consuming cell contents, and were easily quantified as a measure of herbivory. Over the course of 2 weeks, 28 replicates of each of the six mite egg densities were established, 12 using adult thrips and 16 using larval thrips.

We tested for the effects of prey egg density and thrip stage (larva or adult) on the number of mite eggs consumed and feeding scars using a two-way multivariate analysis of variance (MANOVA). We employed the MANOVA approach because the number of mite eggs consumed and feeding scars are not necessarily independent response variables. Where the MANOVA was significant, we proceeded to conduct univariate ANOVAs. Data for feeding scars in the absence of mite eggs (zero eggs treatment) were not included in this analysis because the paired response variable (number of eggs consumed) is absent. We also used linear regression to compare

the number of prey consumed and the number of feeding scars to determine whether there was a negative relationship between feeding on the two different resources.

INDIRECT EFFECTS OF INDUCTION ON PREFERENCE OF THRIPS FOR MITE EGG PREY

The goal of this experiment was to determine whether induced plant resistance would affect spider mites such that eggs from females fed induced foliage would be less preferred than mite eggs from undamaged control plants. Twelve cotton plants were grown until the cotyledons had expanded and then they were randomly divided into two groups: (i) plants inoculated with 20–30 *T. turkestanii* (Ugarov and Nikolski) spider mites, or (ii) undamaged control plants. The number of mites was not exactly controlled (but not biased in anyway) because the goal was simply to damage half of the plants. In previous experiments, *T. turkestanii* was found to be a potent inducer of resistance in young cotton plants (Karban & Carey 1984). After 3 days of feeding, all mites were killed using a non-systemic miticide (dicofol, Kelthane, Rohm and Haas, Co., Philadelphia, Pennsylvania, USA). Plants treated with mites as well as controls were dipped in the miticide. At this stage, the first true leaf was only a bud. After 7–10 days of plant growth, when the first and second true leaves had expanded, all of the plants were infested with 20–30 *T. pacificus* mites. Again, the number of mites was not exactly controlled (but not biased in anyway) because the goal was simply to collect eggs. Eggs produced by adult mites on induced plants are henceforth called 'induced eggs' and eggs produced on control plants are called 'control eggs.' These eggs were used in the two following experiments.

Choice test, prey only. We placed two groups of five mite eggs, one set each of induced and control eggs in 90 mm diameter Petri dishes with moistened filter paper. The position of the groups of eggs was randomized. A larval thrips was introduced to the Petri dish and the dish was sealed. After 3 days, the number of eggs remaining was determined for each group. Over a 2-week period, this experiment was replicated 65 times. For each replicate, the group of mite eggs with more eggs consumed was classified as the preferred prey. The preference of thrips was analysed using a non-parametric sign-test. Replicates in which an equal number of eggs was consumed were omitted from the analysis (Zar 1996).

No-choice test, plant and prey. A second experiment was conducted to test for the effects of mites raised on control and induced plants on omnivory by thrips in the presence of plants. Here, we placed five

control or five induced eggs onto one cotyledon from an unmanipulated plant in a 90-mm diameter Petri dish with one larval thrips ($n=45$, each treatment). After 4 days we counted the number of eggs consumed and the number of feeding scars on the leaves. We tested for the effects of source of the mite eggs (control or induced plants) on the number of mite eggs consumed and feeding scars using a one-way MANOVA.

EFFECT OF INDUCTION ON MITE EGG SIZE AND SUBSEQUENT EFFECTS ON THRIPS PREFERENCE

The aim of these experiments was to determine whether mite egg size was different on induced plants vs. control plants. Control and induced plants were grown as above ($n=12$, each treatment), and the first true leaf was inoculated with 10 adult mites (*T. pacificus*) from the colony. The leaves were examined after 4 days, and the diameter of newly laid eggs were measured using a micrometer. On each of the 24 plants, the diameter of five eggs was measured and averaged as a single data point. The diameter was converted to volume ($4/3 \times \pi \times r^3$; the eggs are spherical), and the effect of induction on egg size was analysed using a *t*-test.

To test whether differences other than egg size contributed to the preference of thrips for control eggs over induced eggs, we conducted a preference test as above (*Choice test, prey only*) while controlling for egg size. Control and induced eggs of equivalent size were measured (220 eggs) using a micrometer and placed in separate groups of five in Petri dishes with one larval thrips ($n=22$). The preference of the thrips was analysed using a non-parametric sign-test.

PLANT COLONIZATION BY THRIPS IN THE FIELD

This experiment was a 2×2 factorial design to detect the effects of induced resistance and prey availability on plant colonization by thrips. Plants were grown in the growth chamber as described above and were assigned to control and induced groups. After mites were removed from the cotyledons with the miticide, the plants were grown until they had two true leaves expanded (14 days). Half of the plants in the control and induced groups were assigned to have prey and were haphazardly inoculated with 30–50 spider mites. Each of the four treatments was replicated 20 times: control, control with mites, induced, induced with mites. After 24 h, these plants were moved to a large cotton field at the University of California, Davis Student Experimental Farm (Davis, California, USA). Cotton plants in this field were large, but had not begun to flower, and the field had a naturally occurring infes-

tation of spider mites and thrips. Experimental plants were placed in the rows, and separated by 1–2 m. After 24 and 72 h we censused each experimental plant in the field for the number of colonizing thrips. This amount of time was not sufficient for the control plants inoculated with mites to induce resistance (A.A. Agrawal, R. Karban, personal observations). The censuses were taken in the cool, early morning, when thrips did not fly off the plants upon disturbance. The number of thrips per plant was averaged for the two census dates. A two-way ANOVA was employed to test for the effects of induced resistance and prey availability on plant colonization by thrips. Six replicates were lost as a result of plant death.

The plants were brought back into the laboratory after the field censuses and were returned to the growth chamber for 3 days to rear thrips. Because thrips lay their eggs in the plant tissue, oviposition (and egg survival) was determined by the number of hatching larvae. Effects of induced plant resistance and prey availability on thrips oviposition was analysed by two-way analysis of variance. The number of mites that colonized the control and induced plants (without mites added) was also recorded to see whether induction had an effect on plant colonization by the mites. The effects of induction on colonization by mites was analysed by a *t*-test.

Results

EFFECTS OF PREY DENSITY ON OMNIVORY

Prey density had a positive effect on the number of prey consumed per thrips (Fig. 1a, Table 1). Although prey density did not have a negative effect on the number of feeding scars on leaves (Fig. 1b, Table 1), there was a significant negative association between prey consumption and plant consumption ($R^2=0.110$, $y=8.426+0.506x$, $F_{1,136}=16.776$, $P<0.001$, Fig. 2). This relationship was unchanged when we only analysed replicates where more than five mite eggs were used.

INDIRECT EFFECTS OF INDUCTION ON PREFERENCE OF THRIPS FOR MITE EGG PREY

Mite egg prey from induced plants were less preferred by thrips than eggs from control plants in experiments where thrips had a choice between induced and control eggs and no leaf tissue was available (sign-test: $P<0.05$, Fig. 3). In the no-choice experiment with mite eggs (control or induced) on non-induced plant leaves, omnivory by the thrips was significantly affected by the source of the mite eggs (Wilks' lambda = 0.923, $F_{2,87}=3.651$, $P=0.030$, Fig. 4). Consumption of eggs from induced plants was reduced by over 50% compared

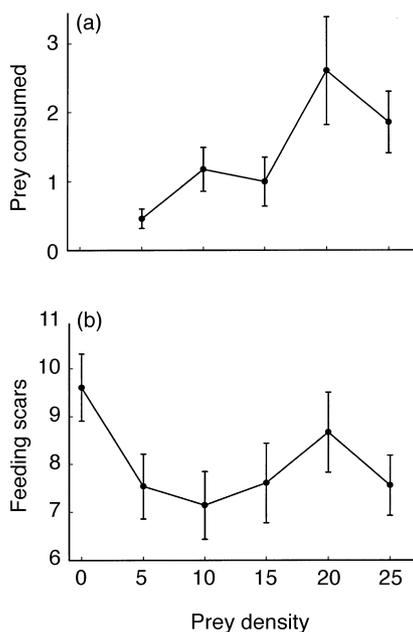


Fig. 1. The effect of prey density on (a) the number of prey consumed, and (b) the number of feeding scars left by thrips. Data shown are mean \pm 1 SE.

to controls (Fig. 4a, univariate analysis: $F_{1,88} = 4.798$, $P = 0.031$). There was no difference in the number of feeding scars on plants with induced eggs compared to plants with control eggs (Fig. 4b, univariate analysis: $F_{1,88} = 1.569$, $P = 0.214$).

EFFECT OF INDUCTION ON MITE EGG SIZE AND SUBSEQUENT EFFECTS ON THRIPS PREFERENCE

On average, eggs from females fed control foliage were 18% larger in volume than eggs from females fed induced foliage ($t = 4.080$, d.f. = 22, $P = 0.031$, Fig. 5a). When egg size was held constant, thrips

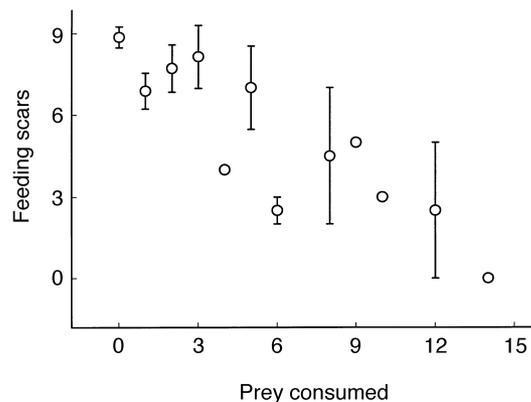


Fig. 2. The relationship between the number of prey consumed and the number of feeding scars left by omnivorous thrips. Data shown are mean \pm 1 SE.

preferred control eggs over induced eggs (sign-test: $P < 0.05$, Fig. 5b). Thus, differences in mite egg size on control and induced plants alone cannot fully explain the preference of thrips for control eggs over induced eggs.

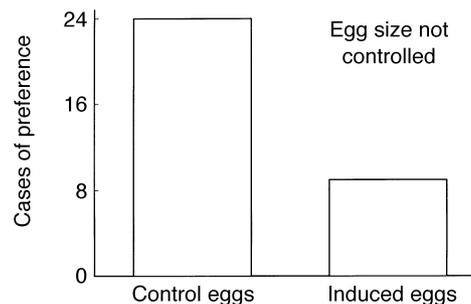


Fig. 3. Preference of thrips for consuming mite eggs from control plants and induced plants in the absence of plants (choice test).

Table 1. Multivariate analysis of variance and univariate analyses for the effects of prey density and thrips stage (larva and adult) on prey consumption and plant consumption

	Source	d.f.	Wilks' lambda	MS	F	P
MANOVA	Density	2, 133	0.909		6.676	0.002
	Stage	2, 133	0.997		0.199	0.820
	Density \times stage	2, 133	0.990		0.703	0.497
Univariate: Prey consumed	Density	1		55.284	9.045	0.003
	Stage	1		2.250	0.368	0.545
	Density \times stage	1		1.207	0.197	0.658
	Error	134		6.112		
Univariate: Plant consumed	Density	1		10.807	0.754	0.387
	Stage	1		2.144	0.150	0.700
	Density \times stage	1		10.807	0.754	0.387
	Error	134		14.334		

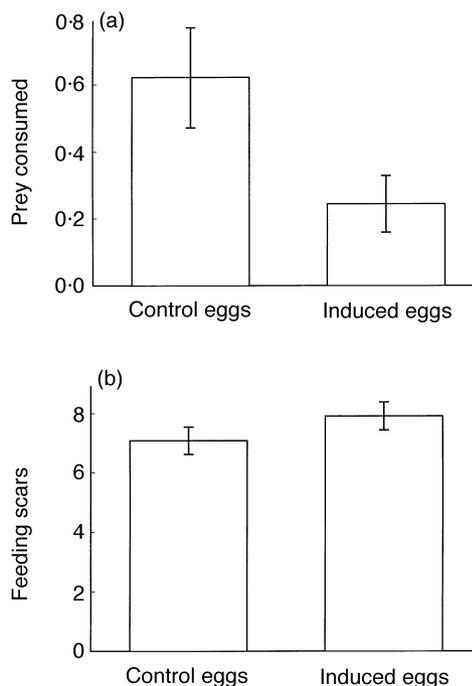


Fig. 4. (a) Consumption of mite eggs, and (b) feeding scars left by thrips on control plants with control eggs or induced eggs (no choice between control and induced eggs). Data shown are mean \pm 1 SE.

PLANT COLONIZATION BY THRIPS IN THE FIELD

Our cotton plants were readily colonized by naturally occurring thrips and spider mites. Induced resistance reduced thrips colonization by nearly 70% compared to controls (Table 2, Fig. 6a). However, this negative effect of induced resistance on thrips colonization was attenuated by the presence of mite eggs (prey) (Table 2, Fig. 6a). The presence of mites in the absence of induced resistance did not affect thrips colonization compared to controls (see Fig. 6a; the significant interaction term in Table 2 indicates that the addition of mites only had an effect for induced plants).

The number of larval thrips that hatched from induced plants was 50% lower than that from control plants (Table 3, Fig. 6b). This effect may have been a result of reduced oviposition on induced plants, or reduced survival of thrips eggs in induced

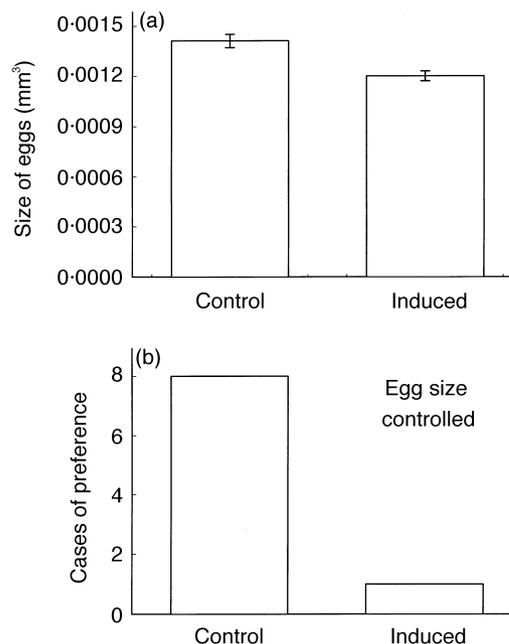


Fig. 5. (a) The effect of induced plant resistance on the size of mite eggs. Data shown are mean \pm 1 SE. (b) Preference of thrips for consuming mite eggs from control plants and induced plants in the absence of plants (choice test) with egg size held constant.

plants compared to controls. Note that the interaction term (induced resistance \times prey availability) was not significant (Table 3), whereas it was significant for plant colonization (Table 2), indicating that mites attenuated the effects of induction on colonization, but not on thrips reproduction. Induced resistance did not affect the number of spider mites that colonized plants (mean \pm 1 SE mites per plant, control = 6.000 ± 1.503 , induced = 8.190 ± 2.315 ; $t = 0.739$, d.f. = 35, $P = 0.465$).

Discussion

TRI-TROPHIC THEORY AND EXPERIMENTS WITH OMNIVORES

Our goal was to combine knowledge of the basic trophic ecology of a common plant–herbivore–omnivore interaction, with the complexities of phenotypic changes that affect the interaction (Price

Table 2. Two-way analysis of variance for the effects of induced plant resistance and prey availability on plant colonization by thrips

Source	d.f.	MS	F	P
Induced resistance	1	19.047	17.189	< 0.001
Prey availability	1	0.925	0.835	0.364
Induced resistance \times Prey availability	1	6.253	5.643	0.020
Error	70	1.108		

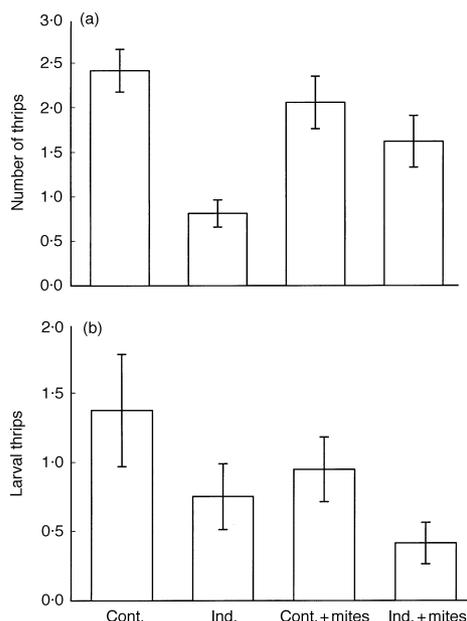


Fig. 6. (a) Thrips colonization of plants placed in the field. Effects of induced plant resistance and mite egg prey availability were assessed in a 2×2 factorial design. (b) Larval thrips emergence from the same plants. The results are the sum of thrips oviposition and successful development of eggs until hatch. Data shown are mean \pm 1 SE. Cont., control; ind., induced resistance.

et al. 1980). We found that manipulation of plant resistance to herbivores can have many direct and indirect effects on omnivory (Fig. 7). We previously showed that induction of resistance caused omnivorous thrips to shift their feeding activities by reducing herbivory and increasing consumption of prey (Agrawal *et al.* 1999a). In the current study, we focused on indirect effects of induced plant resistance. Induced resistance in cotton plants reduces populations of spider mites, and this effect is demographically controlled by adult mites having reduced fecundity on induced plants compared to controls (Brody & Karban 1989). We show that density of mite eggs is positively correlated with consumption rate by thrips. This effect may be a result of differences in prey encounter rates and/or chemical cues given off by the prey. Thus, as induced resistance

reduces mite populations, thrips may reduce their consumption of mites.

Induced resistance also had indirect effects on rates of predation by thrips through changes in the quality of herbivorous prey. Thrips prefer mite eggs produced on control plants over mite eggs produced on induced plants. Although spider mites produced smaller eggs on induced plants compared to controls, this size effect alone did not explain the preference of thrips for control eggs over induced eggs. Rather, mite eggs from induced plants possessed some other characteristics, perhaps chemical in nature, that deterred thrips predation. Although many herbivores are known to sequester plant defences (Duffey 1980), this has not been evaluated for spider mites. One explanation for our result is that herbivores feeding on chemically noxious plants may passively have plant defensive compounds in their tissues, and these may deter predators. Non-sequestering cabbage looper larvae [*Trichoplusia ni* (Hübner)], reared on diets with nicotine from tobacco plants, were protected from predation by Argentine ants [*Linepithema humile* (Mayr)], compared to larvae fed diets lacking nicotine (Cornelius & Bernays 1995). In contrast, genetic resistance of soybean cultivars to herbivorous mites did not influence consumption of mite eggs by predators (Wheatley & Boethel 1992). Tri-trophic theory has long predicted effects of plant variation on members of the third trophic level (Price *et al.* 1980). However, negative effects of induced plant resistance on predators have been rarely reported (Thaler 1999).

When not given a choice, thrips fed less and had higher rates of mortality on induced plants compared to controls (Agrawal *et al.* 1999a). In addition, we found that induced resistance dramatically reduced plant colonization by thrips in the field. This effect was probably not a result of changes in plant morphological or growth characteristics; it was previously shown that cotton plants similarly induced by spider mite herbivory were indistinguishable from control plants in six plant characteristics (Karbon 1987). The negative effects of induced resistance on plant colonization by thrips were almost completely attenuated by the presence of spider mites on induced plants. Thus, thrips appear to utilize environmental information in assessing habitat

Table 3. or the effects of induced plant resistance and prey availability on emergence of larval thrips from plants placed in the field

Source	d.f.	MS	F	P
Induced resistance	1	60.15	4.725	0.033
Prey availability	1	2.619	2.057	0.156
Induced resistance \times Prey availability	1	0.036	0.028	0.868
Error	68	1.273		

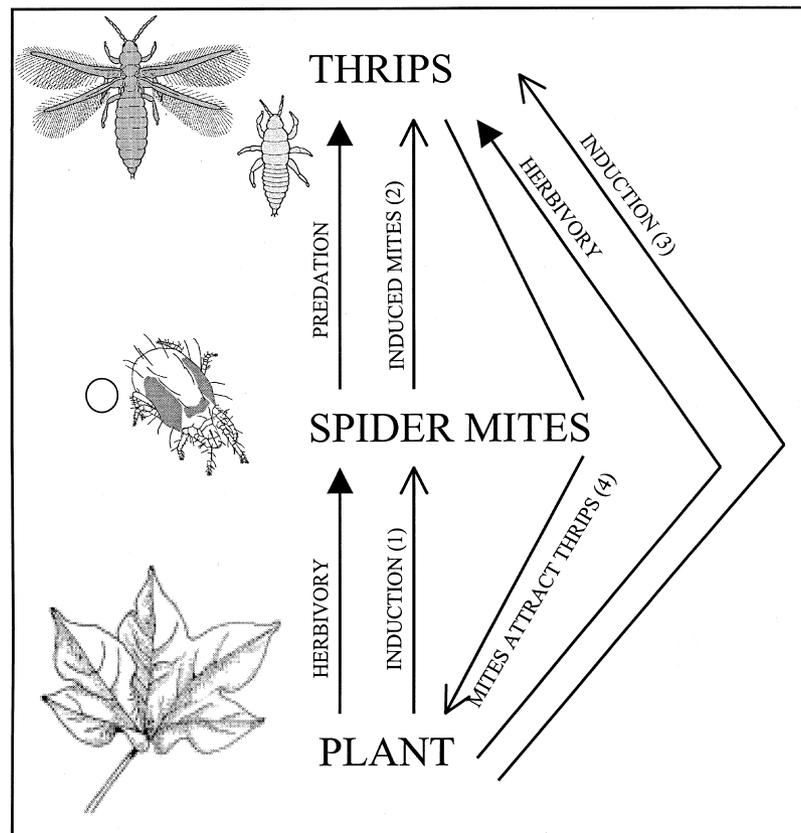


Fig. 7. Interactions between cotton plants, herbivorous spider mites and omnivorous thrips. Solid arrowheads reflect consumption and point to higher trophic levels. Open arrowheads indicate effects of induced plant resistance that were investigated: (1) induced resistance makes spider mites produce fewer, smaller and less attractive eggs; (2) thrips prefer to prey upon spider mite eggs from control plants over induced plants; (3) induced resistance reduces herbivory and colonization of plants by thrips; and (4) the presence of spider mites alleviates the effects of induced resistance on thrips colonization of plants.

quality, and settle to feed where the best food sources are available.

From a plant protectionist perspective, omnivores can be a double-edged sword. On the one hand, western flower thrips are an important crop pest world-wide; on the other hand, they are important predators of mites in some agroecosystems. Our initial hypothesis for the effects of induced resistance on omnivory was motivated by searching for synergism in plant protection. It appeared that induced resistance could be used to reduce herbivory (by both herbivores and omnivores) and increase predation (by omnivores) on herbivores (Agrawal *et al.* 1999a). The current results demonstrate that indirect effects of induction may antagonize the effects of induction on thrips feeding choices. Induced resistance can make plants less attractive to thrips, but also make herbivores less attractive as prey. The net effects of these interactions for herbivore populations should be assessed in the field.

Our other field experiments with induction and omnivory suggest that induction may reduce herbiv-

ory by thrips and promote predation on mites; however, these results are from open field experiments and are confounded by species interactions between mites and thrips and other herbivores, omnivores and predators (Agrawal *et al.* 2000); for example, thrips were less abundant on induced vs. control plants on the first sample after imposing an induction treatment. However, this effect was not observed for the next six sampling dates over 12 weeks, even though induced resistance continued to impact spider mites, whiteflies and aphids. Thus, after a small lag time, thrips were able to compensate for the negative effects of induced resistance. Trichilo & Leigh (1988) found that thrips reproduction was reduced on constitutively resistant cotton varieties compared to susceptible varieties in the laboratory (where no mite prey were available). Negative effects of plant resistance were not observed in their field experiments however, probably because thrips switched from feeding on cotton to feeding on other foods such as mite prey, pollen and nectar (Trichilo & Leigh 1986b). In our experi-

ments, mite populations were reduced by over 50% on induced plants compared to controls (Agrawal *et al.* 2000). This effect was probably mediated by several factors, including direct reductions in mite populations caused by induction of resistance, and indirect reductions in mite populations caused by thrips favouring predation over herbivory. At this stage it appears that induced plant resistance is, at the least, a compatible strategy with biological control by omnivores, and at best, a synergistic tool.

Omnivory in western flower thrips was originally described by several workers studying cotton–arthropod interactions (Gonzalez & Wilson 1982; Trichilo & Leigh 1986a,b, 1988). Working with resistant and susceptible cultivars of cotton, Trichilo & Leigh (1988) showed that several components of thrips performance were reduced on resistant vs. susceptible cotton in the laboratory. Availability of either spider mite eggs or pollen grains attenuated these effects of plant resistance, although pollen was found to be nutritionally superior to mite eggs. Several of our experiments are in agreement with these results, and in addition point to a negative association between the consumption of leaf tissue and mite prey.

Plant quality, prey availability and the presence of conspecifics can also affect the ability of thrips and mites to detect food items. Mite-infested cucumber plants were slightly more attractive to colonizing mites in laboratory trials (Pallini *et al.* 1997). Pallini *et al.* (1997) also found that mites were repelled by plants with *F. occidentalis* (which were competitors and predators). Although we did not address this issue in our field experiment, we did address the converse ecological scenario of mites affecting the preference of thrips. Colonization by thrips was dependent on the quality of the host plant. Control plants with mites were no more attractive to thrips than control plants without mites; however, induced plants with mites were twice as attractive to thrips as induced plants without mites. We interpret this as an adaptive foraging strategy by omnivorous thrips. Where plant quality is bad, colonization depends on availability of alternate foods. Other field studies have recently shown that herbivores can affect the attractiveness of plants to other herbivores (Loughrin *et al.* 1996; Bernasconi *et al.* 1998) and to natural enemies of herbivores (Drukker, Scutareanu & Sabelis 1995; De Moraes *et al.* 1998).

OPTIMAL DIET THEORY APPLIED TO OMNIVORES

Optimal diet theory was developed to form a predictive framework for how organisms with particular morphologies and behaviours would respond to variable environments in order to gather the best foods (Schoener 1971; Westoby 1978; Schoener 1987). Where optimal foods are predictably avail-

able, specialization and even monophagy should be favoured by natural selection. However, generalized diets have advantages, some of which are predicted by optimal diet theory. As outlined by Westoby (1978) animals with a general diet may benefit from: (i) a reduction in search time for food over a small spatial or time scale; (ii) a reduced need for 'resource tracking' of highly available or quality foods over longer periods of time; (iii) sampling different foods when quality cannot be assessed prior to consumption; and (iv) favourable nutrient mixtures from different foods. The fourth hypothesized benefit of omnivorous (or generalized) feeding has been expanded to include the dilution of noxious chemical defences in foods (Freeland & Janzen 1974) and associative feeding benefits where food items interact to facilitate better digestion (Bjorndal 1991).

Many arthropods, including *F. occidentalis*, have broad diets that include feeding on leaves, pollen grains and small arthropods (McMurtry & Rodriguez 1987; Coll 1996; Fagan 1997; Naranjo & Gibson 1996). Westoby (1978) closed his classic paper on the biological basis of varied diet with a plea that future workers consider the application of optimal diet theory to omnivores. Thrips with varied diet selection are likely to benefit from at least the first two hypothesized benefits outlined above. Over the scale of an individual feeding bout on an individual leaf, generalization benefits the thrips when particular foods are not present. Over the season, foods available to the thrips can change dramatically and generalization may be beneficial because a single resource is not required (Gonzalez & Wilson 1982). Finally, a generalized diet allows thrips to assess food quality and select diets with regard to induced plant resistance and its effects on herbivore abundance and quality. It is unknown whether thrips benefit from sampling different foods and diet mixing. Thus, although some questions remain, it appears that optimal diet theory predicts thrips feeding behaviour quite well.

Conclusion

The relative roles of omnivores as herbivores vs. predators is influenced by many factors. In this study we showed that there is a negative association between herbivory and predation in western flower thrips. When plant quality is reduced, thrips become more predaceous. However, induced plant resistance also antagonizes this feeding shift by making herbivorous prey from induced plants less palatable than prey from control plants. Induced plants are less attractive to colonizing thrips than control plants, however, the presence of spider mites alleviates the negative effects of induced resistance. In accordance with optimal diet theory, fine scale variability in the

presence and quality of food items can exert large effects on the foraging of omnivores.

Acknowledgements

This study was primarily supported by the University of California Davis, Young Scholars Program (C.N.K.). We thank Rick Pomeroy and Nu Pham for administrative support. Previous versions of this manuscript were improved by comments from Lynn Adler, Jon Chase, Ramy Colfer, Rick Karban, Jay Rosenheim, Maus Sabelis, Jennifer Thaler and anonymous referees. Carrie Black maintained the mite colonies, Diane Ullman donated the thrips and Arne Janssen provided insect drawings. Financial support was provided by NSF Grant DEB-9701109 and the Center for Population Biology at UC Davis (A.A.A.) and personal funds (C.N.K.).

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Received 5 May 1999; revision received 30 November 1999