Jasmonate-induced plant defenses and prey availability impact the preference and performance of an omnivorous stink bug, *Podisus maculiventris*

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Abstract Many omnivorous insects are important biological control agents, and their success is influenced by both plant resistance and prey availability. The potential impact of these two factors is complicated by the fact that they may not be independent: Resistant plants also often support fewer herbivorous prey. We studied how lifetime development, growth, fecundity and preference of the omnivorous stink bug, *Podisus maculiventris*, was affected by jasmonate-induced plant defenses and amount of prey available. *P. maculiventris* survival was 70 % lower on high-resistance (jasmonate-overexpressing) plants compared to low-resistance (jasmonate-insensitive) plants. However, surviving *P. maculiventris* grew and achieved equal fecundity on low- and high-resistance plants. When given a choice, *P. maculiventris* preferred low-resistance plants, but did not differentiate between caterpillar prey reared on high- or low-resistance plants. Low prey availability impacted distinct aspects of *P. maculiventris* performance: Development time was lengthened, and nymphal and adult mass were reduced, but survival was not impacted. We did not detect any interactive effects between plant resistance and prey availability for any measure of *P. maculiventris*. Thus, we found remarkably compartmentalized impacts of plant resistance and prey availability for this omnivorous insect.

Keywords Host plant resistance · Omnivory · Plant–insect interactions · Tomato · Heteroptera

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Introduction

Omnivores are widely distributed in natural landscapes and employed in biological control, and their biology suggests that their success as predators may be particularly susceptible to plant quality (Coll and Guershon 2002; Eubanks and Denno 1999; Zhi et al. 2006). The predatory activity of omnivores may be impacted directly by host plant resistance through contact or feeding and indirectly via a reduction in the number and quality of herbivorous prey. In addition, prey scarcity may lead to increased plant feeding which could be detrimental on resistant plants (Eubanks and Denno 1999). Although strict predators may also be susceptible to these factors, omnivores are predicted to have more exposure to plant defenses because of their plant feeding and therefore be more strongly affected by these defenses. There is a conflict for successful biological control using omnivores—low-resistance plants frequently attract, provide abundant prey food, and promote survival and population growth of omnivores; however, on low-resistance plants, omnivores may feed more on plants and less on prey (Agrawal et al. 1999).

A recent meta-analysis of the effects of host plant resistance on heteropteran omnivores found that omnivore

abundance in the field is frequently lower on resistant plants (32 % of cases), but performance does not differ (Kaplan and Thaler 2011). Nonetheless, few studies have examined how induced plant defenses influence omnivore performance and how these responses compare to and interact with prey availability. Because herbivorous prey are often less abundance on poor-quality plants, resistant plants and low prey availability are stresses that will likely be encountered simultaneously. There are multiple attributes of performance, and they may be differentially affected by plant quality and prey availability. We studied plant-induced defenses because these defenses are deployed when herbivores feed on the plant and thus when prey feeding by omnivores could benefit the plant.

The jasmonic acid pathway is the major induced defense system in plants that protects against insect attack. The near universal jasmonate pathway signals induced resistance to herbivores from a broad taxonomic range and among nearly all feeding guilds (Creelman and Mullet 1997; Thaler et al. 2002). Chewing herbivores such as caterpillars and beetles, phloem feeders such as aphids (Goggin 2007) and whiteflies (Walling 2000) and cell content feeders such as spider mites and thrips (Li et al. 2002; Thaler et al. 2002) are typically negatively impacted by jasmonate-induced plant defenses. This diversity of effects of the jasmonate pathway is likely linked to the multiple classes of defense traits regulated. For example, in tomato plants, the jasmonate pathway induces trichomes, toxins, digestibility reducers and volatile signals (Kim et al. 2011; Tian et al. 2012). However, little research has been conducted on how jasmonate-induced resistance affects omnivore performance (Zhi et al. 2006).

A few studies have shown that induced plant responses can change omnivore preferences for plants versus prey. Agrawal and Klein (2000) showed that induced resistance in cotton plants caused omnivorous thrips to feed less on plants and more on prey. Herbivore damage also makes cucumber and tobacco plants more attractive to omnivores (Venzon et al. 1999; Kessler et al. 2004). These studies demonstrate the importance of induced plant responses in omnivore preference but do not pinpoint the role of jasmonate defenses. Understanding what kinds of defenses affect omnivores will be important in tailoring plant resistance strategies in agriculture that promote the compatibility of top-down and bottom-up effects.

Here, we investigated the influence of jasmonate-induced defenses of tomato plants and prey scarcity on the lifetime performance and egg production of the omnivorous heteropteran *Podisus maculiventris* (spined soldier bug). *P. maculiventris* consume plant sap with a piercing–sucking stylet (Armer et al. 1998; Lambert 2007), and their feeding damage can induce the jasmonate pathway (Kim et al. 2011). Our previous field experiments showed that

rates of predation by *P. maculiventris* on *Manduca sexta* caterpillars were lower on plants overexpressing the jasmonate pathway compared to plants not expressing the JA pathway (Kaplan and Thaler 2010), indicating that *P. maculiventris* are adversely affected by jasmonate-induced defenses. In this study, we tested the direct (through the plant) and indirect (through changes in the prey) effects of the jasmonate pathway on *P. maculiventris* performance and preference. Specifically, using tomato lines genetically altered in their expression of the jasmonate pathway, we: (1) measured the survival, growth and development time of *P. maculiventris* reared on plants with low, medium and high levels of expression of the jasmonate pathway, (2) tested whether the influence of the jasmonate pathway was altered by the level of prey availability, (3) measured whether expression of the jasmonate pathway influences host plant preference of *P. maculiventris* adults and (4) tested whether *P. maculiventris* adults had a preference for *M. sexta* caterpillars reared on plants expressing low or high levels of the jasmonate pathway.

Materials and methods

Study organisms

Podisus maculiventris were reared in a lab colony originally collected from the forest edge in Ithaca, NY using aggregation pheromone-baited traps. They were maintained on a diet of mealworms and tomato plants. The level of plant resistance via the jasmonate pathway was manipulated using three types of tomato plants that vary in the inducibility of the jasmonate pathway. Wild-type tomato plants (*Solanum lycopersicon* cv Castlemart) that induce the jasmonate pathway following wounding, jasmonate-insensitive mutant plants [*jai-1*; (Li et al. 2004)] that do not induce the JA pathway even when damaged and jasmonate-overexpressing 35S::prosystemin plants that express the jasmonic acid pathway constitutively (McGurl et al. 1994). The jasmonate-insensitive plant is a mutant defective in jasmonate perception that was backcrossed two times into the Castlemart variety, and the jasmonate overexpressor is a transgenic plant developed using agrobacterium-mediated transformation and backcrossed into the Castlemart variety. These lines vary in expression of many plant resistance traits. Jasmonate-overexpressing plants have the highest levels of defensive proteinase inhibitors and polyphenol oxidase (Howe and Ryan 1999), wild-type plants are intermediate, and jasmonate-insensitive plants have the lowest levels (Kaplan and Thaler 2010). Jasmonate-insensitive plants have 87 % fewer total trichomes than wild-type or jasmonate-overexpressing plants and are absent of both the hair-like glandular type-1 trichome and the

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glandular type-VI, (Kaplan and Thaler 2010; Li et al. 2004). Therefore, jasmonate insensitive are the highest quality for many herbivores that are the prey for *P. maculiventris*, wild-type are intermediate and jasmonate over-expressor are the lowest quality (Kaplan and Thaler 2010; Rodriguez-Saona et al. 2010; Scott et al. 2010). Seeds were originally obtained from Gregg Howe (Michigan State University) and propagated by the authors in Ithaca, NY.

Seeds of the three plant types were germinated in plastic trays lined with damp paper towels and covered with plastic wrap. Jasmonate-insensitive homozygous seeds were identified with a diluted methyl jasmonate and ethanol mixture, added just after germination (Li et al. 2004). Seedlings of the three plant types were planted in metro mix soil in 4-inch pots a week after germination. Plants were grown in a climate-controlled growth chamber kept at (26 °C, 14:10 light: dark, 450 microeinsteins of light) until the sixth leaf stage. Plants received water regularly and fertilizer once a week (21:5:20 N:P:K, 150 ppm N). Plants grown in a growth chamber may have lower levels of defense than field grown plants, but the relative rankings of resistance in the three plant types will not be different.

How do host plant resistance and prey availability influence survival, growth and fecundity of P. maculiventris?

We manipulated host plant resistance and prey availability in a factorial design and measured the effects on *P. maculiventris* nymphal survival, growth and development. *P. maculiventris* nymphs were reared from hatching on one of six treatments: jasmonate-insensitive (hereafter, "low-resistance"), wild-type, or jasmonate-overexpressor (hereafter, "high-resistance") tomato plants with either high or low prey availability. All experiments were started with *P. maculiventris* nymphs within 24 h of hatching that were weighed and placed individually into 9-cm-diameter petri dishes with an excised leaflet from the appropriate plant type. Fully expanded leaflets from leaves 4, 5 or 6 were used. Fresh leaflets were exchanged every other day, and the dishes sealed with Parafilm. All nymphs were fed one mealworm (35–60 mg) the day they molted into second instar (first instars do not feed on prey). Nymphs in the high prey availability treatment were given a fresh mealworm every other day; however, if the previous mealworm had not yet been eaten, they were not provided with additional food. Individuals in the low prey treatment were fed 8 days after their last kill. These starvation intervals (2 and 8 days) correspond with lower and upper estimates, respectively, for the length of time between prey meals for wild *P. maculiventris* foraging in the field (Legaspi et al. 1996). Nymphs were observed daily between the hours of 10 am and 1 pm, and the date of each molt and any deaths

were recorded. The experiment was set up in two trials; one in July 2009 (total $n = 119$; n for each treatment $= 13$–26) and one in September 2009 (total $n = 120$; n for each treatment $= 14$–24). Within each trial, newly hatched individuals were set up over a 2-week period with nymphs equally allocated on each day to plant type and prey availability treatments. Individuals from trial 2 were weighed on the first day of the third and fifth instars. *P. maculiventris* were kept in the study, and the plant resistance and prey availability treatments were maintained until the individual died. Adult mass was measured 3 days after adult eclosion in both trials. The number of days from egg hatch to eclosion was measured as nymphal development time. Trial 1 ran for a total of 86 days from hatching, and trial 2 ran for a total of 71 days at which point 94 % of the individuals had died.

To test whether nymphal rearing conditions carried over to affect adult performance, the 35 nymphs that survived to adulthood in the second trial were used to assess fecundity. One week after adult emergence, a male was randomly selected from the colony and added to each petri dish with a female from the experiment. The adults were maintained on low-resistance plants with high prey availability. Dead males were replaced with a new individual from the colony. Petri dishes were checked each day for egg masses. Egg masses were put into individual petri dishes on a moistened filter paper. The number of eggs, date they were laid, the number that hatched, and hatch date were recorded. The day of death was recorded to determine adult lifespan.

We used Cox proportional hazards regression model (Cox and Oakes 1984) to assess how plant resistance and prey availability affected nymphal survival. We present the main effects of treatments and their interactions and coefficients for survival models as hazard ratios (exp[b_i]) and standard errors. We used MANOVA to analyze third instar, fifth instar and adult mass in trial 2. When the overall MANOVA was significant, we conducted two-way ANOVAs testing the effects of plant resistance and prey availability on the individual time points. Because we had adult mass and nymphal development time for both trial 1 and trial 2, following MANOVA, these responses were analyzed using three-way ANOVA including trial. Two-way ANOVA was used to analyze adult longevity and fecundity in trial 2.

Plant choice assay

Since plant resistance affected performance of nymphs (see "Results"), choice assays were conducted to determine the preference of adult *P. maculiventris* for low and high-resistance plants. Cages (24 in 3 cages, Bugdorm 2, Bio-Quip, Inc) were established with one low-resistance plant and one high-resistance plant set side by side approximately 30 cm apart. Tomato plants at the 7–10 leaf stage in

four-inch pots were paired with plants of the other plant type based on similar size and shape. Three freshly killed mealworms (head crushed) were placed on each plant (*P. maculiventris* eat recently dead prey). One *P. maculiventris* adult was selected randomly from the colony, their sex was recorded, and placed on the floor of the cage, directly between the two pots. The position (on or off of the plant) and behavior (resting, moving, plant feeding) of the *P. maculiventris* adult was recorded 1 min after being placed in the cage and every 10 minutes for 1.5–2 h. Between three and five cages were watched at a time in nine observation periods over 2 months from February to April 2010. Forty-six predators were observed.

We measured several components of plant choice: the amount of time on each plant type, the number plant feeding events on each plant type and the amount of time spent moving and resting while on a plant. Mealworm prey were rarely eaten so this behavior was not included in the analysis. We analyzed the plant choice and plant feeding data using a Pearson's Chi-square test with the null hypotheses that *P. maculiventris* would choose and plant feed equally between the low- and high-resistance plants. Signed-rank test was used to analyze the proportion of observations moving and resting.

Prey choice assay

Host plant resistance can also change the quality of herbivorous prey, so we tested whether the *P. maculiventris* adults had a preference for *M. sexta* caterpillars depending on whether caterpillars had been reared on low-resistance or high-resistance plants. *M. sexta* were grown for 6 days on each plant type when second instar individuals were matched for mass to the nearest 4 mg and offered to adult *P. maculiventris* in 90-cm petri dishes. *M. sexta* caterpillars were labeled with a dot of paint on the horn, switching the color used for each treatment between replicates, so we could identify the source of the caterpillar. The *P. maculiventris* were withheld prey for 24 h prior to experimentation to ensure hunger. Each dish was continuously observed for 20 min, and the first caterpillar attacked was recorded (one *P. maculiventris* did not eat a caterpillar and was excluded from the analysis; none ate more than one caterpillar). Twenty-four replicates were conducted, and the paired choices were analyzed using a sign test.

Results

Performance on high- and low-resistance plants

Survival until adulthood was strongly affected by plant resistance but not affected by prey availability. Survival was greatest on low-resistance plants where it took more

than 20 days for 25 % of the nymphs to die, compared to wild-type and high-resistance plants where 25 % of the nymphs died within 4.5 days (Fig. 1; Table 1). On low-resistance plants, 55 % of nymphs successfully reached adulthood compared to only 20 and 14 %, respectively, on the wild-type and high-resistance plants (Fig. 1). There was no interaction between plant resistance and prey availability (Table 1).

P. maculiventris mass was not affected by the level of plant resistance (Fig. 2; overall MANOVA plant resistance: $P = 0.27$; Table 2); in contrast, low prey availability decreased mass (overall MANOVA $P = 0.03$; Table 2). Mass was not different between nymphs in the low and high prey availability treatment when they entered the third instar, but was lower in the low prey treatment in the fifth instar and in adulthood (Table 2). Similar to mass, nymphal development time was not affected by plant
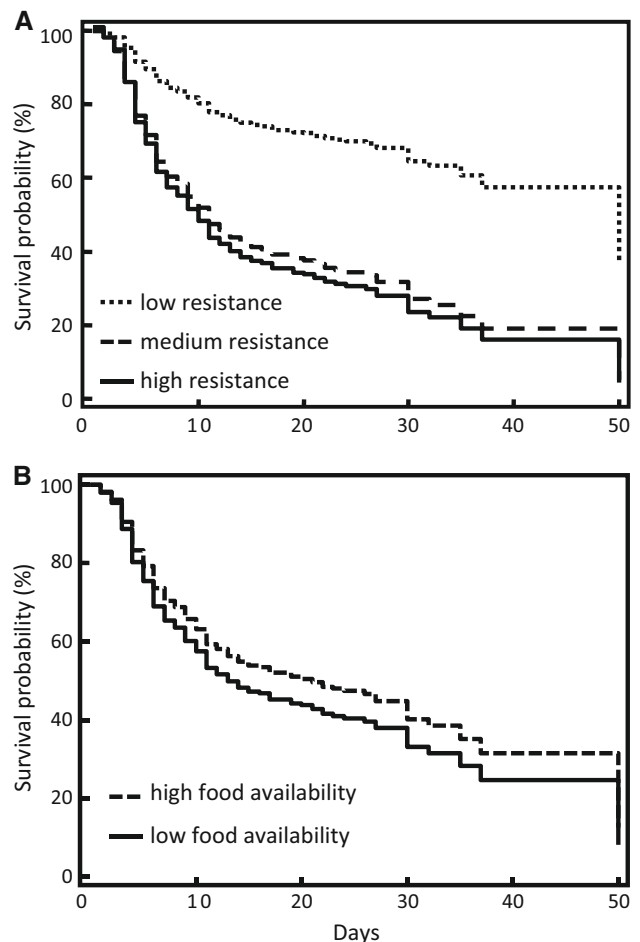

Fig. 1 The probability of nymphs surviving until adulthood. Survival was assessed daily starting when the individuals were 24-h old until they died. **a** On the low (jasmonate insensitive), medium (wild-type) and high-resistance (jasmonate-overexpressor) plants and **b** in the low (one mealworm every 8 days) and high (one mealworm every 2 days) prey availability treatments

Table 1 Results from Cox proportional hazards analysis of effect of plant type and food availability on nymphal survival

	β	CI	P
Plant type (wild-type)	1.23	0.89–1.71	0.21
Plant type (low-resistance)	0.55	0.37–0.81	0.002
Food availability (starve)	0.76	0.53–1.09	0.14
Wild-type × starve	1.26	0.79–2.011	0.33
Low-resistance × starve	0.71	0.39–1.27	0.25

Plant type uses the high-resistance plant as the baseline. Food availability uses the fed treatment as the baseline. The interactions between plant type and food availability are shown as the interaction between wild-type × starve and low-resistance × starve. β hazard ratios

Table 2 Effects of plant resistance and prey availability on mass (mg) of third and fifth instar *Podisus maculiventris* nymphs and adults and total nymphal development time

| Factor	df	F	P
Mass third instar			
Plant resistance	2	0.088	0.96
Prey availability	1	0.17	0.68
Plant × prey	2	0.082	0.45
Error	62		
Mass fifth instar			
Plant resistance	2	0.99	0.38
Prey availability	1	3.95	0.051
Plant × prey	2	0.56	0.57
Error	59		
Mass Adult			
Plant resistance	2	0.34	0.71
Prey availability	1	8.73	0.0046
Plant × prey	2	0.46	0.63
Trial	1	1.92	0.0080
Error	54		
Development time			
Plant resistance	2	1.47	0.23
Prey availability	1	100.80	<0.001
Plant x prey	2	1.59	0.21
Trial	1	7.41	0.17
Error	72		
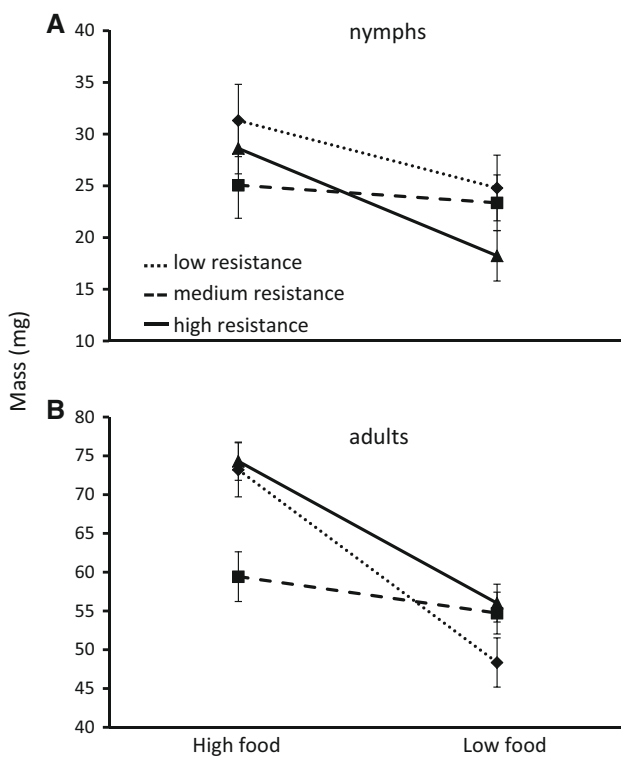
Fig. 2 The mass (mg) of *P. maculiventris* at **a** fifth instar nymphs and **b** 3 days after reaching adulthood in the low (one mealworm every 8 days) and high (one mealworm every 2 days) prey availability and plant resistance treatments (low = jasmonate insensitive, medium = wild-type, high = jasmonate overexpressor). Markers indicate the mean ± 1 SE

or the plant resistance × prey availability interaction ($P = 0.87$). Males and females lived the same length of time ($P = 0.38$). Only four of the females that had been fed on the low prey diet during development reached adulthood, and one
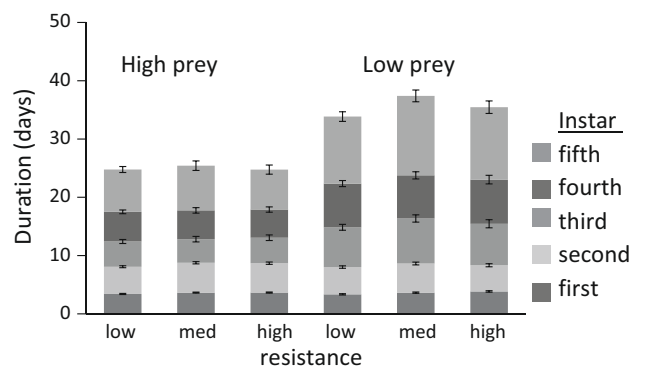

Fig. 3 The mean duration (days) of the five nymphal instars in the low (one mealworm every 8 days) and high (one mealworm every 2 days) prey availability and plant resistance treatments (low = jasmonate insensitive, medium = wild-type, high = jasmonate overexpressor). Instar was recorded daily for the duration of the experiment. Each *bar* indicates the mean ± 1 SE

resistance, but was increased 23 % by low prey availability (Fig. 3; Table 2). We did not detect interactions between plant resistance and prey availability on mass at any time point (Table 2).

Aside from adult mass, other components of adult performance were not affected by the plant resistance or prey availability treatments. Adult lifespan was not affected by plant resistance ($P = 0.99$), prey availability ($P = 0.74$),

of these laid eggs so they were excluded from the fecundity analysis. Fourteen females laid eggs within the fed treatment, but neither egg production or number of successfully hatched eggs were affected by plant resistance (total egg production: $P = 0.98$; percent egg hatch: $P = 0.60$).

Plant choice

Because plant resistance had such a strong effect on the performance of *P. maculiventris* nymphs, we tested whether plant resistance affected adult preference. Of the 46 *P. maculiventris* adults observed, 18 were found on the low-resistance plants and eight were found on the high-resistance plants (Pearson's Chi-square: $P = 0.049$). Of the *P. maculiventris* that were observed on a plant, the average percentage of time intervals spent on the plant was 41.03 % (SE $\pm$ 6.43) on the low-resistance plants and 30.67 % (SE $\pm$ 11.08) on the high-resistance plants (Wilcoxon signed-rank test: $T = 2.46$, $P = 0.013$). More *P. maculiventris* choose to plant feed on the low-resistance compared to the high-resistance plants. Out of 46 observed *P. maculiventris*, ten fed on the low-resistance plant and two fed on the high-resistance plant (Pearson's Chi-square: $P = 0.03$). All *P. maculiventris* plant fed only once at most and never on more than one plant. Of the *P. maculiventris* that were observed on the plants, there was no difference in the percentage of time intervals spent moving on the high- and low-resistance plants ($F_{12} = 0.077$, $P = 0.78$) or resting ($F_{12} = 0.35$, $P = 0.57$).

Prey choice

Because plant resistance can indirectly affect omnivores through the consumption of poorer quality prey, we tested whether rearing prey on high- or low-resistance plants changed their acceptability to adult *P. maculiventris*. *P. maculiventris* did not differentiate between size-matched *M. sexta* caterpillars that had been reared on low-resistance (10 chosen) or high-resistance plants (13 chosen) (Sign test: $P = 0.68$).

Discussion

We report that impacts of plant resistance and prey availability are remarkably compartmentalized across the lifetime development for this omnivorous insect. Plant resistance reduced *P. maculiventris* survival, whereas low prey availability increased development time and reduced mass gain. In all nymphal instars, *P. maculiventris* survival was highest on low-resistance plants and lowest on wild-type and high-resistance plants. The higher mortality on the high-resistance plants was most pronounced in the early

instars and resulted in 40 % fewer reaching adulthood. However, the individuals that reached adulthood had similar performance as we did not detect an effect of plant resistance on adult mass, lifespan or fecundity. These divergent effects of the two stresses suggest that plant resistance does not affect the omnivore simply by reducing food availability, early instar nymphs are directly killed by the plant resistance traits, but do not appear to be affected by them later in life. The lack of effect of plant resistance on performance of surviving *P. maculiventris* is consistent with the results of a meta-analysis of the effects of plant resistance across many heteropteran omnivores (Kaplan and Thaler 2011).

In contrast to plant resistance, prey availability did not influence *P. maculiventris* survival, but low prey availability increased development time and reduced mass gain. Given that many polyphagous predators, including *P. maculiventris* (Legaspi and Oneil 1993, 1994a, b), are adapted to patchy food resources, maintaining survival in the face of infrequent prey meals may be the norm for this group. In a study on a closely related species, *Podisus nigrispinus*, Holtz et al. (2009) found that low prey availability reduced adult fecundity. Surprisingly, in our study, there were no interactions between plant quality and prey availability on omnivore performance, highlighting that plant resistance and food availability act via different routes. The independent effects of these two stresses highlight the divergent responses of omnivores to plant and prey food. These results also demonstrate the importance of measuring multiple performance traits across the omnivore's lifetime to understand how different stresses affect the organism.

The reduced survival of nymphs on resistant plants corresponds with reduced preference of *P. maculiventris* adults for high-resistance plants. As adult *P. maculiventris* did not show a preference for size-matched *Manduca sexta* caterpillar prey reared on high- or low-resistance plants, differences in preference appear to be driven by direct effects of plant resistance rather than indirect effects via changes in prey quality. In a study where *P. maculiventris* was fed *M. sexta* prey that had been fed on artificial diet with and without plant allelochemicals, *P. maculiventris* performance was reduced when there was both poor-quality prey and prey were scarce (Weiser and Stamp 1998). While *M. sexta* are not known to sequester plant secondary compounds (Self et al. 1964; Wink and Theile 2002), they can have increased allelochemical concentrations in their hemolymph (Barbosa et al. 1991; Strohmeyer et al. 1998). This indicates that the omnivore can be affected by allelochemicals they encounter via the herbivore, and under some conditions, plant resistance and prey availability do interact to affect the omnivore.

Other studies have also found lower predation of soft-bodied arthropods by *P. maculiventris* on resistant plants.

For example, a field cage no-choice experiment found that groups of *M. sexta* caterpillars on high-resistance tomato plants were eaten less than caterpillars on low-resistance plants (Kaplan and Thaler 2010). Similarly, *P. maculiventris* ate fewer Mexican bean beetles on resistant compared to susceptible soybean cultivars (Bartlett 2008). Since both of these studies were of short duration (several days), it suggests that *P. maculiventris* preference for low-resistance plants is what causes reduced predation on larvae.

While a large literature demonstrates the importance of the jasmonate pathway in resistance to chewing herbivores such as beetles or lepidopterans, there is less known on how the jasmonate pathway affects heteropterans, whether herbivorous or omnivorous. Several studies show that the jasmonate pathway provides resistance to herbivorous heteroptera. For instance, the mirid bug, *Tupiocoris notatus*, fed more on jasmonate-deficient wild tobacco plants compared to tobacco with intact defenses (Paschold et al. 2007). In contrast, cis-jasmone application to soybean plants did not affect attraction or population size of the herbivorous stink bug *Euschistus heros* (Vieira et al. 2013). A small number of studies have also tested the effects of the jasmonate pathway on omnivorous heteroptera. Many omnivorous heteroptera, including *P. maculiventris* (Lambert 2007), are negatively affected by trichome presence (Coll and Ridgway 1995), a trait which is regulated by the jasmonate pathway in many plant species. A specific jasmonate-regulated compound, cystatin, interferes with *P. maculiventris* midgut enzyme activity, but this did not affect their growth and development (Alvarez-Alfageme et al. 2007). Similarly, omnivorous *Perillus bioculatus* was not affected by a jasmonate-inducible proteinase inhibitor present in the diet of its prey (Bouchard et al. 2003).

Implications for biological control and trophic interactions

Survivorship of omnivorous *P. maculiventris* was the greatest on the same plant types where herbivory is typically greatest, plants with defective jasmonate signaling. In a scenario where *P. maculiventris* can choose between high- and low-resistance plants, this could increase biological control because the *P. maculiventris* will eat most prey on plants that are not otherwise defended by resistance traits. Our results also suggest that if older nymph move to resistant plants, their survival and performance should not be reduced. Agren et al. (2012) modeled how plant quality alters the ability of omnivores to control herbivore populations and found that the outcome is very sensitive to whether the omnivore shifts its behavior to feed on the plant or on the herbivore when on a low-quality plant. Our result suggests these omnivores would feed equally on prey coming from high- or low-quality plants but that if given a choice they would leave the low-quality plants altogether. In a mixture where high- and low-resistance plants were both available, omnivores may move to low-resistance plants which is also where the herbivores are likely most abundant.

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