

# Effects of prey availability, facultative plant feeding, and plant defenses on a generalist insect predator

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**Abstract** This study examined the effects of feeding interval, access to host plants (thus, a source of sap), and plant defenses on the predatory insect, *Podisus maculiventris* Say (Hemiptera: Pentatomidae). The experiment consisted of a 2 × 2 design with two feeding intervals (1 day or 5 days) and predators living on either tomato plants or plastic plants. Females fed every day had greater body weights and egg hatch rates than females fed every five days. Females on tomato plants lived longer than females on plastic plants. However, access to plants did not alleviate the effects of low prey level on predator weight or reproductive output. In a second experiment, third instar nymphs were placed on either tomato plants or plastic plants for four days to examine the effects of tomato trichome defenses on these predators. Nymphs on tomato plants experienced 50% mortality compared to 15% mortality for nymphs on plastic plants. Some nymphs living on tomato plants were trapped by the hairy trichomes of the plant; others had gummed up legs from the exudates of the plants' glandular trichomes, which inhibited their movement and ability to feed on prey. Although predators appeared to benefit from feeding on tomato plants, their ability to live on the plants was negatively affected by the defensive features of the plants. The potential effects of

trichome defenses on predator survival and population dynamics must be considered when evaluating the benefits of plants on insect predator life histories and efficacy as biological control agents.

**Keywords** Hemiptera · Indirect effects · Pentatomidae · *Podisus maculiventris* · Prey scarcity · Tomatoes · Trichomes

## Introduction

Plants and herbivore natural enemies are often assumed to have indirect, but coupled relationships where plants provide shelter and a food source for predators, and predators provide herbivore regulation for plants. Many arthropod predators directly benefit from plants by facultatively feeding on them, presumably to obtain moisture or nutrition (Valicente and O'Neil 1995; Gillespie and McGregor 2000; Coll and Guershon 2002). Plant feeding may enable predators to colonize systems before prey arrive and facilitate predator persistence when prey are scarce (reviewed in Naranjo and Gibson 1996), and can also enhance predator growth and survival. For example, plant feeding increases the nymphal development rate of the mirid, *Dicyphus hesperus* Knight (Hemiptera: Miridae) (Gillespie and McGregor 2000). Predatory stinkbugs, *Podisus maculiventris* Say (Hemiptera: Pentatomidae), provided either tomato or potato leaves lived longer than those provided only water (Valicente and O'Neil 1995). However, the work showing the benefits of plant feeding for predators has been conducted primarily using abscised leaves in microcosms (Valicente and O'Neil 1995; Crum et al. 1998; Gillespie and McGregor 2000), and relevant knowledge about the effects or benefits of plant feeding when it occurs on plants is lacking.

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Beside facultative plant feeding, natural enemies can indirectly benefit from plants by using volatile defensive chemical of plants for prey location (Karban and Baldwin 1997; Vet and Dicke 1991 and references therein). However, host plant defenses are not always beneficial to predators and can have negative effects. Plant trichomes and secretions can interfere with the search movement of small natural enemies and reduce their foraging efficiency (Karban and Baldwin 1997). Green lacewings move slower on tobacco, which is well defended with trichomes, than on cotton, which has relatively few trichomes (Elsely 1974). The movement of coccinellid beetles searching on tobacco is inhibited by the plants' hairy trichomes (Elsely 1974; Belcher and Thurston 1982) and exudates from tobacco trichomes inhibit the movement of *Trichogramma* wasps (Rabb and Bradly 1968). Eisner et al. (1998) found that coccinellid beetles, preying on aphid pests of the plant *Mentzelia pumila* Nutt., were incapacitated by the plants' trichomes. In observations of stink bug predator movement on tomato plants, I found, and report here, that tomato trichomes interfere with nymphal searching ability and reduce predator survival.

Little is known about the effects of plant feeding and plant defenses on predatory insects when living on plants, especially under prey scarce conditions. *Podisus* predators are strong candidates for use as biological control agents against pests in solanaceous crops because of their broad host range (Tipping et al. 1999; De Clercq et al. 2000), but this plant family is often well defended with trichomes, potentially interfering with predator efficacy. The objectives of this study were: (1) to determine the effects of varying feeding regimes on the weight, reproduction, and longevity of female *P. maculiventris* living on plants, (2) to determine the effects of living on tomato plants (and plant supplemental feeding) on the weight, reproduction and longevity of female *P. maculiventris* living on plants, and (3) to determine what direct effects tomato plant defenses have on *P. maculiventris* nymphs. I hypothesized that an increased feeding interval would negatively affect predator weight, reproduction, and longevity, but access to plants—and resultant plant feeding—would alleviate these effects. I hypothesized that the tomato trichomes would reduce nymphal movement on the plant and nymphal survival due to the incapacitating effects of the trichomes.

## Materials and methods

### Study organisms

The stink bug, *Podisus maculiventris*, is a ubiquitous predator in both natural and agricultural environments (McPherson et al. 1982). This predator experiences periods

in which prey densities are low (Mukerji and LeRoux 1969), which in turn, can have negative effects on its growth, reproduction, and survival (Evans 1982; Legaspi and O'Neil 1994; Crum et al. 1998). These predators have several adaptations that enable them to survive periods of prey scarcity including energy trade-offs, whereby they forego reproduction, reducing energy expenditures, and so increasing the likelihood of survival when prey are scarce (O'Neil and Wiedenmann 1990; Legaspi and O'Neil 1993). Also, like several other heteropteran predators, *P. maculiventris* facultatively feeds on plants (Ruberson et al. 1986; Crum et al. 1998).

Tomatoes, *Lycopersicon esculentum* Mill., have allelochemical and glandular and non-glandular trichome defenses (Luckwill 1943), which confer resistance against invertebrate herbivores (Levin 1973; Duffy and Isman 1981). Rutin, chlorogenic acid, and methyl ketones are released from the glandular trichomes as a sticky exudate (Duffy and Isman 1981) and have been shown to have negative effects on insect herbivores and their predators and parasitoids (Campbell and Duffy 1979; Traugott and Stamp 1997). The exudate gums up the legs of insect herbivores causing immobilization and/or death.

### Insect and plant maintenance

The stink bugs used for the experiments were obtained from the USDA laboratory in Beltsville, Maryland and the Maryland Department of Agriculture (Annapolis, Maryland). The bugs were fed mealworm larvae [*Tenebrio molitor* L. (Coleoptera: Tenebrionidae)] and supplied with a cotton ball moistened with water. The colony was maintained at 26:15°C with a 14L:10D photoperiod, which is representative of the mean maximum and minimum temperatures and photoperiod in mid-summer (July) in Binghamton, New York (National Climatic Center, 1979).

Tomato plants, *Lycopersicon esculentum* Mill. (var. Heinz), were cultivated from seed in flats in a greenhouse under a 14L:10D photoperiod. Seedlings were transferred to 250 ml pots with Agway pro-mix soil containing time released fertilizer (0.9% N, 0.9% P, 0.9% K), and watered as needed. All plants used in the experiments were at least 36 cm in height and were replaced before flowering.

In a preliminary experiment, I evaluated the time adult predators spent resting, searching, and feeding (time spent with beak inserted in plant tissue) on plants to determine if predators would come into contact with tomato trichomes or feed on plants. Newly eclosed females were randomly placed on either the adaxial surface of a leaf, abaxial surface of a leaf, or on the stem of tomato plants (n = 25). Plants were placed in cages (37 cm diameter, 40 cm height) made with aluminum screen (1 mm × 1 mm mesh

size) to prevent the predators from escaping. Predators were observed for one hour after being on the plants for 48 h and again after 96 h. Percent of time spent resting, searching, and feeding on plants was recorded. Predators spent 75% of the time resting, 11% searching, and 12% feeding on plants. There was no difference in time allocation between the 48 h and 96 h observations (resting,  $T = 1.20$ ,  $P = 0.24$ ; searching,  $T = 0.30$ ,  $P = 0.77$ ; feeding,  $T = 0.67$ ,  $P = 0.50$ ; Wilcoxon paired-sample test).

#### Effects of tomato plants on body weight, reproduction, and longevity of stink bugs

To determine the effects of tomato plants on the body weight, reproduction, and longevity of *P. maculiventris* under different feeding intervals, newly eclosed unmated females were weighed and assigned to one of the following treatments: 1) plastic plant and fed daily ( $n = 17$ ), 2) plastic plant and fed every 5 days ( $n = 16$ ), 3) tomato plant and fed daily ( $n = 19$ ), and 4) tomato plant and fed every 5 days ( $n = 19$ ). Plastic plants obtained from a local craft store were used as controls; they were similar in size and architecture to the tomato plants. Plants were placed in cages (37 cm diameter, 40 cm height) made with aluminum screen (1 mm  $\times$  1 mm mesh size) to prevent the predators from escaping. The prey abundance levels were: abundant prey (fed every day) and scarce prey (fed every 5 days). The prey scarcity regime of 5 days was selected because these predators commonly go several days without feeding when prey are scarce (O'Neil 1988). To feed the predators, each predator was taken off the plant and placed in a 500 ml plastic container with two large ( $\sim 18$  mg fresh weight) mealworms. On average, the bugs attack  $\sim 0.5$  prey per day in field situations (Wiedenmann and O'Neil 1992), so they were given two large mealworms to ensure an abundant food supply. The predators were allowed to feed for  $\sim 2$  h, which is the average handling time for these predators (Wiedenmann and O'Neil 1991), and then placed back into their assigned treatment. Predators from all treatments were taken off plants daily and placed in 500 ml plastic containers to standardize treatments. The plants were sprayed daily with a fine mist of water to provide moisture for the predators. The thermal regime in the greenhouse was  $\sim 26:15^\circ\text{C}$  with a photoperiod of 14L:10D. Lights were turned on as needed during the experiments to maintain the photoperiod. On the fifteenth day after the predators were placed on the plants, they were removed from the cages and weighed. For mating, females were placed in a 500 ml plastic container with a male, and continued on their previous feeding regime in an environmental chamber set at  $26:15^\circ\text{C}$  with a 14L:10D photoperiod. The first clutch of eggs from each female was collected and reared until

hatching. Only the first clutch was used because subsequent clutches might have exhibited less of an effect due to the longer time spent off the plants. A cotton swab moistened with water was placed with each clutch of eggs to provide moisture. After hatching, hatch rate was recorded.

The dependent variables measured were fresh weight of females immediately after they were taken off the plants, longevity of females from ecdysis to death, number of eggs laid in the first clutch, percent of eggs that hatched (first egg clutch), and average weight of progeny. The initial fresh weight (weight of newly eclosed females before they were placed on the plants) was used in the analysis as a covariate with the dependent variable of fresh weight after plant treatment. The initial fresh weight was also tested as a covariate with the variables number of eggs laid, percent of eggs that hatched, and longevity, but was not significant and was therefore dropped from the analysis of these dependent variables to conserve degrees of freedom. All response variables were analyzed with SPSS 14.0 statistical software (LEAD Technologies, Inc.) using a fixed-effects factorial ANOVA (two levels of prey availability  $\times$  two levels of plant type). To meet the assumptions of ANOVA, the dependent variable percent of eggs that hatched was arcsine square-root transformed (initial data was highly skewed). All other variables met ANOVA assumptions and untransformed data are presented.

#### Direct effects of tomato trichomes on predators

While observing the behavior of *P. maculiventris* on tomato plants, I discovered that many of the nymphs could not move through the dense trichomes of the tomato plant. After being on the plants for four days, more than 50% of the nymphs were dead or immobilized by the trichomes. To determine the extent to which tomato trichomes affect the movement of nymphs on the plants, third instar nymphs were placed on tomato plants or plastic plants (as a control). The third instar was used because it is a middle stage in the nymphal development of these predators. An aluminum screen cage (40 cm height  $\times$  37 cm diameter, 1 mm mesh size) was placed over each plant to prevent predators from escaping. The predators were kept on the plants without access to food for 4 days (to keep them searching for food), and plants were sprayed daily with water to provide moisture for the insects. The nymphs were observed for one hour at 48 h and 96 h after being placed on the plant. During the hour observation, the nymphs were checked to see if their movement was impeded by the trichomes. After four days, each nymph was taken off the plant and placed under a dissecting microscope to determine if the legs were gummed with the exudates from the tomato trichomes. There were a total of 30 nymphs

observed for tomatoes and 15 nymphs for plastic plants. Colony egg hatch declined during this experiment, which limited nymph availability—more nymphs were placed in the trichome treatment to ensure that sufficient individuals would be available for microscopy.

## Microscopy

Micrographs of the legs and ventral surface of insects that died on the plants were compared with micrographs of nymphs on the plastic plants to determine the effects of the tomato exudates. To prepare for electron microscopy, dead nymphs were first placed in a fixative consisting of 3% glutaraldehyde in 0.1 M phosphate buffer with pH 7.0 for 4 h at room temperature. They were then dehydrated in a series of ethanol dilutions and then critical point dried. All material was mounted and gold sputter coated for 30 s. The material was observed with an Etec Autoscan scanning electron microscope operating at 10.0 kV.

## Results

### Effects of prey availability on body weight, reproduction, and longevity

Final adult fresh weight and percent of eggs that hatched were affected by feeding interval (Table 1). Females fed daily weighed, on average, 9 mg more than females fed every 5 days. Females fed daily also had a 50% greater egg hatch rate compared to females fed every 5 days. However,

feeding interval did not affect the number of eggs laid or adult longevity (Table 1).

### Effects of tomato plants on body weight, reproduction, and longevity

The type of plant that predators lived on had an effect only on adult longevity (Table 1). Females on tomato plants lived 8 days longer than females on plastic plants. No other variables were affected by plant treatment. Further, access to live plants did not alleviate the effects of low prey availability on weight, reproduction, or survival (i.e., no interactive effects). Predators in the tomato plant treatment were regularly observed feeding on plants, often having their beaks inserted into leaves for up to 15 min.

### Direct effects of tomato trichomes on predators

The tomato trichomes proved to be lethal to the nymphs. Of 30 nymphs, 27% died within two days of being placed on the plant. Furthermore, 47% died by the fourth day on the plant. For nymphs on plastic plants, only one nymph died by the second day (6.7%) and two (13.3%) by the fourth day. Many of the nymphs that died on the tomato plants were entrapped in the long non-glandular trichomes on the stem of the plant, and did not come in contact with the shorter glandular trichomes. This entrapment was caused by the mechanical defensive features of the non-glandular trichomes, which trap insects, rather than the 'sticky' chemical features of the glandular trichomes.

**Table 1** Effects of prey availability and plant type on the final adult weight (fresh weight of females), number of eggs, percent of eggs that hatched, and adult longevity of predatory stink bugs

	Independent variable			
	Final adult weight (mg)	# of eggs	% egg hatch	Adult longevity (days)
<i>A. Mean ± SE for main effects</i>				
Prey availability				
Every day	68.8 ± 1.6	16.4 ± 2.3	60.0 ± 7.0	30.8 ± 1.8
Every 5 days	59.4 ± 2.7	12.8 ± 2.4	29.3 ± 8.2	32.4 ± 2.1
Plant type				
Tomato plant	62.4 ± 2.2	12.2 ± 2.2	50.0 ± 7.8	35.6 ± 1.8
Plastic plant	66.2 ± 2.3	17.1 ± 2.5	39.4 ± 7.4	27.7 ± 2.2
<i>B. ANCOVA and ANOVA results</i>				
Prey availability	$F_{(1, 57)} = 6.1, P = 0.017$	$F_{(1, 64)} = 1.1, P = 0.291$	$F_{(1, 40)} = 8.6, P = 0.007$	$F_{(1, 58)} = 0.3, P = 0.576$
Plant type	$F_{(1, 57)} = 0.7, P = 0.794$	$F_{(1, 64)} = 2.2, P = 0.143$	$F_{(1, 40)} = 1.0, P = 0.331$	$F_{(1, 58)} = 7.7, P = 0.007$
Interaction	$F_{(1, 57)} = 0.8, P = 0.367$	$F_{(1, 64)} = 0.1, P = 0.876$	$F_{(1, 40)} = 2.6, P = 0.114$	$F_{(1, 58)} = 0.1, P = 0.733$

Predators were placed on either tomato plants or plastic plants and fed either every day or every five days. Means ± standard errors (SE) (A) and ANOVA results (B) are given

However, several of the nymphs that were still alive were affected by the exudates from the glandular trichomes. Of the nymphs that were still alive, 31% were stuck to the plant. Six of the remaining nymphs repeatedly fell off the plants during the observation time due to the excessive gumming on their legs from the glandular exudates. When the live nymphs were viewed under a dissecting scope after the trials were completed, all were found to have gummed legs from the trichome exudates.

The electron micrographs also showed that the legs of the nymphs on tomato plants (after four days) had considerable gumming compared to the non-gummed legs of nymphs never placed on tomato plants (Fig. 1a–c). The tarsal claw (seen in Fig. 1a), which predators use to hold on to the plant, was completely encased, rendering it unusable (Fig. 1b). The same gumming was observed on nymphal leg hairs (Fig. 1d). These leg hairs were mostly or completely covered over with the trichome exudates.

## Discussion

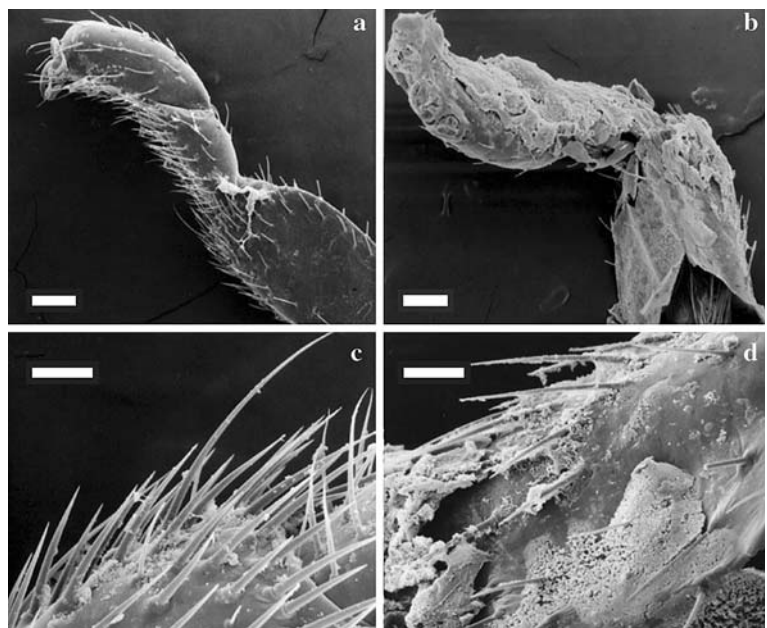
An increased feeding interval had negative effects on predator body weight and egg hatch rate, but not on number of eggs laid or longevity—these results are consistent with other studies. For example, Crum et al. (1998) found that body weight and egg production decreased with low prey abundance, but longevity did not. Adult *P. sagitta* F. (Hemiptera: Pentatomidae) body weight and reproduction were reduced by prey scarcity, but longevity increased (De Clercq and Degheele 1992). Some studies suggest that *Podisus* predators are adapted to prey scarcity, where under

prey scarce conditions predators reduce their reproductive output and transfer the energy to maintain body weight (O’Neil and Wiedenmann 1990; Legaspi et al. 1996). Although predators did not maintain body weight in my study, they did live just as long as well-fed individuals. During prey scarcity, the ability to survive may be just as, or even more important than maintaining body weight, as the former increases the probability of finding prey over time.

In most studies, the reduced reproductive output was generally a reduction in the number of eggs that were laid (De Clercq and Degheele 1992; Legaspi and O’Neil 1994; Crum et al. 1998). While females may reduce costs by laying fewer eggs than well-fed females, I found that females fed less frequently showed significantly reduced hatch rates. Faced with insufficient nutrition, fewer resources may have been allocated to the eggs of poorly fed females.

Studies examining the benefits of facultative plant feeding for insect predators have yielded equivocal results. Ruberson et al. (1986) found that survivorship and adult weight benefited from a plant supplemented diet, but others have found that the addition of plant material to *P. maculiventris* diets had either a neutral or negative effect on nymphal growth and development (Crum et al. 1998; Weiser and Stamp 1998). In this study, living on tomato plants (and presumably using plant sap as a dietary supplement) did not provide a strong benefit for predators—only longevity was enhanced for females living on tomato plants. More importantly, access to live plants did not alleviate the effects of low prey availability on reproduction and weight of females. Under field conditions, plant

**Fig. 1** (a) Electron micrograph of the leg of a third instar nymph that was never on a tomato plant (scale bar = 100  $\mu$ m). (b) Electron micrograph of the leg of a third instar nymph that was on a tomato plant for 4 days. The tarsal claw is completely covered with exudates from the glandular trichomes (scale bar = 100  $\mu$ m). (c) Electron micrograph of the hairs on the tarsi of a third instar nymph that was never on a tomato plant. The arrow points to the tarsal claw (scale bar = 600  $\mu$ m). (d) Electron micrograph of the hairs on the tarsi of a third instar nymph that was on a tomato plant for two days (scale bar = 600  $\mu$ m)



feeding may not have as great a benefit when prey are scarce as has been shown in some laboratory experiments, except to aid in predator ability to persist during prey scarce conditions. However, my design did not partition plant feeding and trichome defenses into different treatment, so I cannot definitively say that plant feeding did or did not have an ameliorative effect. Since predators on live plants were also exposed to trichomes, the detrimental effects of the trichomes could have masked any beneficial effect that plant feeding may have had on body weight or reproduction. Studies using plants, with and without trichome defenses, are necessary to elucidate the relative effects of plant feeding and trichomes on insect predators. Further, choice tests using plants with and without trichome defenses can show whether predators discriminate among such plants when searching for prey or locating oviposition sites.

Why did females on tomato plants live longer than females on plastic plants? Valicente and O'Neil (1993) found similar results where predators with access to plant supplement and water lived significantly longer than predator without access either, and suggested that predators were obtaining moisture from plants, which enabled them to live longer. However, they did not separately evaluate the effects of water or plant supplement in predator diets, so it is unclear which had a greater impact on survival. In my study, predators on both tomato and plastic plants received water, but only predators on tomato plants had the opportunity to feed on plants. Predators on plastic plants were observed feeding on water droplets, whereas predators on tomato plants were observed feeding both on water droplets and leaves (beaks inserted into leaves). Hence, the increase in longevity seen only on tomato plants suggests that access to plants (and presumably plant feeding), not water alone, provides temporary nutritional or other, unknown resources that can facilitate predator persistence.

Most studies have investigated the benefits of a plant supplemented diet by feeding abscised plant parts to predators. As shown in this study, only confining predators on intact plants manifested the detrimental effects of the plant trichome defenses—gumming of nymph legs and tarsi and a 34% increase in nymph mortality. The gumming of the legs caused two problems for the nymphs; first, several of the nymphs became stuck to the plant, and secondly, several of the nymphs repeatedly fell off the plant. Similar effects were also observed with adults (A. Lambert, unpub. data). Although I did not test first or second instar nymphs, it is likely that mortality would be much higher because of their small size. Both glandular and non-glandular trichomes of wild and cultivated tomatoes [*L. pennellii* (Corr.) and *L. esculentum*, respectively] caused mortality of potato aphids, *Macrosiphum euphorbiae* (Thomas) (Goffreda et

al. 1998), which are smaller than first instar *P. maculiventris*. Shade et al. (1975) found that exudates of glandular trichomes block the spiracles of some insects and adhere to larvae, preventing them from moving. The gumming over of these hairs would not only reduce the ability of these predators to move, but would also reduce their ability to properly perceive their environment. The leg hairs are used as sensory structures and aid in adhering to surfaces (Gullan and Cranston 2000). In one instance, I observed an adult female unable to insert her beak in a *T. molitor* larvae due to the gumming on her tarsal claws, which prevented her from gripping the surface. I observed many body parts, primarily on insect ventral surfaces, that were gummed with exudates, including abdominal and thoracic segments and beaks.

Yang (2000) showed that both predator body size and plant architecture are important in the movement ability of *P. maculiventris*. *Podisus* predators actively search for prey, increasing the likelihood of predators coming into contact with to the defensive features of trichome-bearing plants. Tomato stems are especially replete with trichomes (Wilkins et al. 1996)—the effects of such plant traits on the searching ability (especially among plants) of actively searching predators must be determined. Since *P. maculiventris* is a generalist predator, it may have a 'loose' association with the host plants on which it searches for prey and may lack the adaptations necessary to withstand trichome defenses.

Until now, there has been no documentation of plant defenses having an adverse effect on insect predator survival. In the case of *P. maculiventris*, which are common in both natural and agricultural environments (McPherson et al. 1982), it is assumed that since they are found in these environments, they are endemic and effective predators in them. However, the ability of *P. maculiventris* and other hemipteran predators to build up or maintain stable populations on trichome-rich plants still must be determined. Further, previous studies looking at the use of plants by *P. maculiventris* have been done in the laboratory using only plant parts (Ruberson et al. 1986; Valicente and O'Neil 1995; Crum et al. 1998; Weiser and Stamp 1998), and predators most likely did not come in contact with the structural defenses of the plants. This study shows that investigations of the impact and benefits of plants on insect predators must take into account the whole structure of the plant, ensuring a more accurate evaluation of the influence of plants on predator life histories.

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