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How to cite this manuscript

If you make reference to this version of the manuscript, use the following information:

Bayoumy, M. H., Osman, M. A., & Michaud, J. P. (2014). Host plant mediates foraging behavior and mutual interference among adult Stethorus gilvifrons (Coleoptera: Coccinellidae) preying on Tetranychus urticae. Retrieved from http://krex.ksu.edu

Published Version Information

Citation: Bayoumy, M. H., Osman, M. A., & Michaud, J. P. (2014). Host plant mediates foraging behavior and mutual interference among adult Stethorus gilvifrons (Coleoptera: Coccinellidae) preying on Tetranychus urticae (Acari: Tetranychidae). Environmental Entomology, 43(5), 1309-1318.

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Digital Object Identifier (DOI): doi:10.1603/EN14134

Publisher's Link: http://ee.oxfordjournals.org/content/43/5/1309

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Host Plant Mediates Foraging Behavior and Mutual Interference Among Adult *Stethorus gilvifrons* (Coleoptera: Coccinellidae) Preying on *Tetranychus urticae*

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ABSTRACT Physical plant characteristics can influence predator foraging and their behavioral responses to each other. This study examined the searching efficiency and functional response of adult female *Stethorus gilvifrons* Mulsant foraging for *Tetranychus urticae* Koch (Acari: Tetranychidae) on castor bean, common bean, and cucumber leaves. Experiments conducted on leaf discs in arenas for 12 h revealed a type II functional response for *S. gilvifrons* on all host plants. Per capita searching efficiency and killing power decreased with increasing predator density on all plants, but most notably on common bean, the plant with the highest prey consumption rates, due to greater mutual interference. Attack rates were highest on common bean and lowest on castor bean, whereas handling times were shortest on common bean and longest on cucumber, such that the daily predation rate was maximal on common bean. Host plant interacted with predator and prey densities to affect searching efficiency and functional response, the differences in mite consumption among host plants increasing with predator and prey densities. The waxy layers of castor bean leaves and high trichome counts of cucumber leaves appeared to reduce predator foraging efficiency. Thus, the efficacy of *S. gilvifrons* against *T. urticae* is likely to be greatest on plants such as *Phaeseolus vulgaris* L. that have relatively smooth leaves.

KEY WORDS area of discovery, attack rate, density-dependence, functional response, handling time

Biological control of phytophagous mites by predators might benefit from a better understanding of the factors influencing predator-prey interactions. One approach is to study a predator's searching efficiency and its functional response to changes in prey density, as these are often indicative of biocontrol efficacy (Fathipour et al. 2006, Bayoumy 2011, Bayoumy and Michaud 2012) and may be useful in predicting biological control outcomes (Timms 2008). A predator's functional response describes its pattern of prey consumption over a range of prey densities (Holling 1959) and its mathematical form provides insight into the dynamics and stability of the predator-prey interaction (McCann et al. 2005). Numerous models have been proposed to characterize density-dependent predator-prey dynamics. One of the simplest is the Nicholson and Bailey (1935) model that defines the 'area of discovery' (a_t) as the average area searched by a predator 'a' during the search time 't', a measure of predator searching efficiency that remains constant and independent of prey and predator densities. However, it was later challenged by an inductive model (Hassell and Varley 1969) that suggested the searching efficiency of a predator declines exponentially as its own density increases (e.g., via intraspecific aggregation). This consideration led to the incorporation of a mutual interference constant (m) (Hassell 1971). Although not without limitations (Skalski and Gilliam 2001), Hassell and Varley's model (1969) is still widely employed because of its simplicity (Veeravel and Baskaran 1997).

The morphology and biochemistry of plants can influence predation and parasitism of the herbivores that feed on them (e.g., Messina and Hanks 1998) and many arthropod predators respond to the physical or chemical properties of the plants that bear their prey (e.g., Skirvin and Fenlon 2001, Michaud 2012). Although plant features may provide information with respect to prey availability, they may also hinder foraging behavior (Vet and Dicke 1992). Plant morphology (hairs, trichomes, waxes) and chemistry (toxins, exudates) can impede predator movement and prey capture (e.g., Stavrinides and Skirvin 2003), thus influencing patch residence time, attack rate, and searching efficiency (Coll et al. 1997). Glandular trichomes (Eisner et al. 1998), leaf hairiness (Treacy et al. 1987), and the presence of cuticular waxes (Eigenbrode et al. 1996) have all been shown to affect predator abundance and prey consumption rates. The host plant may also influence predator functional response via effects on prey palatability (Sabelis et al. 1999) or the provision of refuges (Kreiter et al. 2003). It is therefore important to understand potential interactions between predator density

and host plant traits that may be antagonistic or synergistic with respect to biological control outcomes.

Biological control of spider mites has centered on two groups of biological control agents, predatory mites in the family Phytoseiidae, and various species of Stethorini (Coleoptera: Coccinellidae) (Biddinger et al. 2009). Predatory mites, with their short life cycles and low food requirements, are generally more effective than insect predators in controlling pest mites because of their ability to utilize alternative food sources and search efficiently for prey at low population levels (McMurtry et al. 1970). However, several species of the genus *Stethorus* have received considerable attention as spider mite predators because of their demonstrated potential to exert control in specific settings such as fruit orchards (Biddinger et al. 2009). Chazeau (1985) summarized the general biology of Stethorini and reported that 40% of the 68 species attacked spider mites of economic importance and, in some cases, regulated pest mites below economic levels. They are generally characterized as voracious predators, with both larvae and adults feeding on all mite life stages with high efficiency (Chazeau 1985).

Stethorus gilvifrons Mulsant (Coleoptera: Coccinellidae) is a predator of the two-spotted spider mite, *Tetranychus urticae* Koch (Acari: Tetranychidae), a cosmopolitan pest of vegetable and fruit crops (Wilkerson et al. 2005). Experimental releases of *Stethorus punctillum* Weise to suppress *T. urticae* in greenhouses resulted in establishment and pest suppression on pepper and cucumber plants, but failed on tomato plants due to the presence of trichomes (Raworth 2001). The functional and numerical responses of *Stethorus* spp. to various mite species and environmental factors have also been examined (e.g., Houck and Strauss 1985, Haji-Zadeh et al. 1994, Matter et al. 2011, Osman and Bayoumy 2011). In this study, experiments were designed to evaluate the influence of host plant type on the response of adult *S. gilvifrons* females to varying densities of spider mites and foraging conspecifics. Castor bean, *Ricinus communi*s L., common green bean, *Phaseolus vulgaris* L., and cucumber, *Cucumis sativus* L., are all important crop plants in Egypt that suffer spider mite infestation and differ in leaf surface features (Dabrowski and Marczak 1972). Common green bean (cultivar Bronco) has small, dark green leaves with a relatively low density of hooked trichomes and a relatively smooth surface texture, whereas castor bean (cultivar GCH6), has large, palmately lobed leaves with a glabrous, very waxy surface texture. By contrast,

cucumber (cultivar Tamra 761) has large, triangular leaves covered with a high density of trichomes. The hooked trichomes on some *Phaseolus* cultivars (e.g., *P. lunatus*) can have detrimental effects on insects and mites (Kavousi et al. 2009; Riddick and Wu 2011). Trichome-based plant resistance to herbivores can be either compatible (Rott and Ponsonby 2000, Loughner et al. 2008) or incompatible (Riddick and Wu 2011) with biological control.

Phytoseiids and many other mites occur preferentially on the lower (abaxial) surfaces of leaves and field observations confirm that nearly 98% of mite predators are distributed on abaxial leaf surfaces (Sudo and Osakabe 2011). Therefore, our predation measurements focused on the abaxial leaf surface. The identification of plant substrates that do not limit the predation potential of *S. gilvifrons* would improve rearing capacity and help the natural enemy industry expand the production of this predator for augmentative releases. It is known that coccinellids may express preferences for particular plant species independent of the presence of prey (e.g., Schmidt 1992), and may utilize induced plant volatiles for prey location (Ninkovic 2001), but there are no reports of phytochemistry influencing foraging efficiency, so these were not the focus of the present study. Rather, the objective was to determine whether the different leaf surface traits of these selected plant species affect the behaviour of *S. gilvifrons* when foraging for *T. urticae*.

Materials and Methods

Stock cultures. A stock colony of two-spotted spider mite, *T. urticae*, was maintained on seedlings of common bean, *Phaseolus vulgaris* L., grown in soil in plastic pots (25 cm diameter) in wooden-framed cages ($100 \times 50 \times 60$ cm) covered with nylon mesh. The cages were held at 28 ± 3 °C, $75 \pm 10\%$ RH, and 14:10 L:D photoperiod with illumination (4000 lux) provided by fluorescent lamps. New plants were introduced as required.

Pupae of *S. gilvifrons* (n = 63) were collected from castor bean plants infested with *T. urticae* in Mansoura district, Egypt and held individually in Eppendorf tubes (Eppendorf Gerätebau Netheler & Hinz GmbH, Oldenburg, Germany) in an incubator at 25 ± 1 °C, $70 \pm 5\%$ RH and 16:8 L:D photoperiod until adults emerged. The adults were then introduced into a cage (as above) with common bean plants bearing prey at 28 ± 3 °C, $75 \pm 10\%$ RH, and 14:10 L:D photoperiod. Other cages (as above) were maintained beetle-free as a source of

mite-infested plants for periodic introduction into the beetle colony. Predators used in the experiment were reared in continuous culture for approximately two generations under the same laboratory conditions as their prey. Experiments were conducted only with adult females, as these are the most voracious life stage.

Leaf morphology. A series of leaves (n = 10) of each of three developmental stages was randomly selected for examination from each plant species. Leaves ca. six weeks of age were removed from upper, middle and lower sections of randomly selected plants. Leaves of similar size (7–8 cm in width at the widest point) were selected from each plant species for measurements of trichome density and wax thickness. Trichome numbers (straight and hooked) were counted on the abaxial leaf surface of each leaf under a stereomicroscope (10x magnification) over an area of 1 cm^2.

To measure leaf thickness, leaf pieces containing the midrib were cut from terminal leaflets (n = 10) of each plant species and fixed in formalin and acetyl alcohol for 48 h (10 ml. formalin, 5 ml glacial acetic acid and 85 ml ethyl alcohol 70%), washed in 50% ethyl alcohol, dehydrated in ethanol and embedded in paraffin wax with a melting point of 56 °C (Sass 1956). A rotary microtome was used to cut sections 15 μ thick. These were stained with crystal violet erythrosine and mounted with balsam on glass slides (Nassar and El–Sahha 1998). The thickness of different leaf tissues was measured using a stage micrometer under a compound microscope at 400x magnification.

Experimental arena. The arena consisted of a leaf disc ($\approx$ 6.0 cm^2) placed adaxial surface down on water-soaked cotton in a plastic Petri dish (8.5 cm diameter) ventilated by means of a hole in the lid (1.0 cm diameter) covered with organdy mesh. A piece of filter paper separated the leaf disc from the cotton. Eggs of *T. urticae* were transferred from the stock culture onto the leaf discs and eclosing nymphs were permitted to develop to the adult stage. To preclude oviposition in experimental arenas, newly molted adult *T. urticae* (< 2 h old; at 25 °C, *T.urticae* adults do not oviposit until they are 36-48 h old) were transferred directly to fresh experimental arenas of each leaf type (n = 80 per leaf disc). To minimize the influence of the host plant used in rearing (common bean) on predator responses, *S. gilvifrons* pupae were collected from the stock culture and isolated in Petri dishes. As adults emerged, they were provisioned daily with *ad libitum T. urticae* adults on 2.0 cm^2 leaf discs of one of

the three plant species on which mites had been permitted to settle, for 24 h prior to experiment. Beetles were then starved for another 24 h before their use in the consumption experiments to standardize hunger levels. Thus, all beetles used in the experiments were 48 h old. All experiments were conducted at 25.0 ± 1.0 °C, 70 ± 5 % RH and 16:8 L:D photoperiod.

Estimation of consumption. In order to measure the effects of leaf surface type on foraging behavior, adult *S. gilvifrons* females (≤ 48 h old) were placed in groups of one, two, three, four, five, six, or seven individuals per arena (n = 10 replicates per treatment). Each arena contained one leaf disc bearing 80 *T. urticae* newly molted adults (< 2 h old). Prey consumed were not replaced and if the predator had escaped, the data were discarded. After 12 h, the predators were removed and the numbers of remaining intact and killed prey were counted. All mites killed by beetles were completely consumed (Chazeau, 1985). Consumption estimates were adjusted downward by the mean mortality observed in control arenas of each plant type at the same prey density, but without predators.

The area of discovery (a_t) was estimated according to Hassell (1978) as follows:

$$a_t = 1/P \log_e N/N - N_a \tag{1}$$

where 'a' is the area of discovery at the time of exposure 't', 'N' the number of prey offered, 'N_a' the number of prey consumed, and 'P' the number of predators introduced.

Model (1) was used to correlate the area of discovery to prey density, but was inappropriate for correlation with predator density, as it assumes each parasitized host gives rise to a new parasitoid, which is not true in a predator–prey system. To account for mutual interference among predators and variation in area of discovery, the model of Hassell and Varley (1969) was used as follows:

$$a_t = QP^{-m} \tag{2}$$

where 'a' is the area of discovery at time 't', 'Q' is the quest constant (area of discovery with one predator searching), 'm' is the mutual interference constant (slope of the regression of

loga_t on log P), and 'P' is the number of predators. Expressed in logarithms, the equation becomes linear as follows:

$$\log a_t = \log Q - m \log P \tag{3}$$

The k-value, or 'killing power' (Ooi 1980), is the difference between the logarithms of the population before and after mortality (Varley et al. 1973):

$$K\text{-value} = \log_{10}(N/S) \tag{4}$$

The consumption data on different host plant leaves at $25 \pm 1°C$, 70 ± 5 % RH and 16:8 L:D photoperiod were used to generate functional response parameters at seven prey densities (11, 13, 16, 20, 27, 40, 80 adult *T. urticae*). The procedure of Juliano (2001) was used to analyze predator functional response. Type of response (type I, II, or III) was determined using a polynomial logistic regression of the proportion of prey consumed versus the initial number of prey offered, as follows:

$$\frac{N_a}{N_0} = \frac{\exp(P_0 + P_1 N_0 + P_2 N_0^2 + P_3 N_0^3)}{1 + \exp(P_0 + P_1 N_0 + P_2 N_0^2 + P_3 N_0^3)} \tag{5}$$

where N_a is the number of prey consumed, N_0 is the initial prey density, and the parameters P_0, P_1, P_2, and P_3 are the constant, linear, quadratic, and cubic parameters, respectively, related to the slope of the curve. Maximum likelihood estimates of parameters P_0 to P_3 were obtained by logistic regression using the Proc CATMOD procedure of SAS (SAS Institute 2000).

The curve of N_a / N_0 has a negative exponential shape in a type II response, whereas it is dome-shaped in a type III response. These curves may both be fit by either quadratic or higher order polynomial expressions. In some cases, the model was reduced by omitting the quadratic or cubic terms until all remaining coefficients were significant (Juliano 2001). If the linear term was not significantly different from 0, a type I functional response was indicated,

whereas a significant negative value indicated type II, and a significant positive value, type III (Juliano 2001). The initial analysis indicated that our data fit a type II response on all host plants, so all further analyses assumed a type II response. The second analysis used a nonlinear least squares regression, Proc NLIN (SAS Institute 2000), to estimate parameter values (T_h and either a for type II, or b, c, and d for type III). Because the experiment was carried out without replacement of prey, the appropriate model for a type II functional response is the 'random-predator' equation (Rogers 1972):

$$N_a = N_0 \left\{ 1 - \exp\left[a \left(T_h N_a - T \right) \right] \right\} \tag{6}$$

where T is the time of exposure, a the attack rate, and T_h the handling time. Values of T_h were used to calculate the maximum attack rate (T / T_h) by individual *S. gilvifrons* during 24 h (Hassell 2000).

      Statistical analyses. Values for number of prey consumed and killing power were subjected to a two-way ANOVA with predator density and host plant as fixed factors (SigmaPlot 2004). In the event of a significant interaction, a separate one-way ANOVA was conducted for each independent variable. Leaf surface traits were subjected to one-way ANOVA. Means were separated using the Bonferroni test ($\alpha = 0.05$) whenever data were normally distributed and variances were homogeneous (Shapiro-Wilk test). To homogenize error variance, data were square root-transformed before analysis.

      Relationships between predator density and area of discovery on various leaf types were analyzed by linear regression (SigmaPlot 2004). To test for equality of slopes and intercepts of regression lines, parallel line analysis was conducted (SigmaPlot 2004). This macro tests the linear regressions of multiple XY pair data sets to determine if the line slopes and intercepts are significantly different ($\alpha = 0.05$). After a and T_h were determined, the differences from the original data (m_t) and the differences between a and T_h values were tested for significance by estimating variance using the jackknife technique (Meyer et al. 1986). The jackknife pseudo-value (m_j) was calculated for the n samples using the following equations:

$$m_{ja} = n m_{ta} - (n - 1)\, m_{ia} \tag{7}$$

$$m_j T_h = n m_t T_h - (n - 1)\ m_i T_h \qquad\qquad (8)$$

The mean values of (n - 1) jackknife pseudo-values (m_i) for a and T_h for the predator on each host plant were subjected to ANOVA. The significance level ($\alpha = 0.05$) was adjusted for multiple comparisons using the Bonferroni correction, a/n, where n = the number of paired comparisons.

Results

There were significant effects of both predator density ($F_{6,189} = 168.15$, $P < 0.001$) and host plant ($F = 13.01$; df = 2, 189; $P < 0.001$) on total prey consumption and a significant 'prey density*predator density' interaction ($F = 2.31$; df = 12, 189; $P < 0.01$). Total mite consumption by *S. gilvifrons* females increased with predator density on castor bean ($F = 134.23$; df = 6, 63; $P < 0.001$), common bean ($F = 118.39$; df = 6, 63; $P < 0.001$) and cucumber ($F= 165.95$; df = 6, 63; $P < 0.001$), the increase being curvilinear and convex on all leaf types (Fig. 1A). However, prey consumption per predator decreased significantly as predator density increased and varied among leaf types, particularly at higher predator densities (Table 1). There were significant effects of predator density ($F = 191.13$; df = 6, 189; $P < 0.001$), host plant ($F = 18.08$; df = 2, 189; $P < 0.001$) and 'prey density*predator density' interaction ($F = 1.15$; df = 12, 189; $P < 0.05$) on k-values. The killing power (k-value) increased significantly with predator density on all host plants (castor bean: $F = 63.61$; df = 6, 63; $P < 0.001$; common bean: $F = 54.82$; df = 6, 63; $P < 0.001$; and cucumber: $F = 86.13$; df = 6, 63; $P < 0.001$, Fig. 1B). There were significant effects of predator density on area of discovery on common bean and cucumber ($F = 11.76$; df = 1, 68; $P < 0.001$ and $F = 11.14$; df = 1, 68; $P < 0.001$, respectively), but not on castor bean ($F = 0.58$; df = 1, 68; $P < 0.05$, Fig. 2). As predator density increased from one to seven individuals, the area of discovery decreased on leaves of common bean more than on castor bean (test for equality of slopes $F = 3.85$; df = 1, 136; $P < 0.05$) indicating that more mutual interference, estimated by equation (3), occurred on common bean (Fig. 3). Neither common bean nor castor bean were significantly different from cucumber with respect to change in area of discovery with

predator density ($F = 0.29$; df = 1, 136; $P > 0.05$ and $F = 2.56$; df = 1, 136; $P > 0.05$, respectively).

Polynomial logistic regression revealed that both the number and proportion of prey consumed by *S. gilvifrons* females on all three plant types fit a type II functional response model with significantly declining slopes (Table 2, Fig. 4A, B). Estimates of functional response parameters revealed significant differences among attack rates and handling times on the different leaf types ($F = 17.3$; df = 2, 3; $P < 0.05$ and $F = 298.2$; df = 2, 3; $P < 0.001$, respectively) with the highest attack rate and the lowest handling time observed on common bean (Table 3). The maximum number of *T. urticae* consumed by a single beetle in 24 h (T / T_h) was 46.2, 58.5 and 44.4 adult mites on castor bean, common bean and cucumber, respectively.

Common bean leaves possessed hooked trichomes on their abaxial surfaces, but at relatively low density (Table 4). Trichomes, both straight and hooked, occurred on cucumber leaves at more than nine times the density of common bean. In contrast, the leaves of castor bean were much thicker than those of the other species and were devoid of all trichomes, but covered with conspicuous layers of cuticular wax.

Discussion

The results of this study illustrate the role of the host plant in mediating predator–prey interactions via short-term density-dependent effects on predator foraging behavior. Predator consumption and killing power increased with predator density on all host plants, supporting the intuitive inference that high predator densities will increase rates of prey consumption overall. However, increasing the number of predators per patch did not result in a proportional increase in the number of prey consumed due to the effects of mutual interference, as noted in other studies (Henne and Johnson 2010, Bayoumy and Michaud 2012). Typically, the *k*-value of a predator increases with its abundance, resulting in more prey consumption (Ooi 1980). Partial consumption of prey at higher prey densities was not an issue. For example, Houck (1991) examined the functional response of *Stethorus punctum* (LeConte) to *T. urticae* and found that the handling time of starved beetles was increased due to more thorough extraction of body fluids from each prey. However, adults of this species pierce the mite cuticle and

siphon out the contents, whereas female *S. gilvifrons* consume mites entirely, cuticle and all, so incomplete consumption was not observed, nor was there variation in extraction of nutrients from prey as a function of satiation. The observed decrease in searching efficiency with increasing predator density indicates increasing mutual interference among predators (Fig. 3). This is likely due, in part, to confinement in arenas generating high conspecific encounter rates. Clearly, such data cannot be extrapolated to field conditions, but do suggest that predator aggregation will increase negative interactions.

Searching efficiency declines as predator density increases because each spends more time interacting with conspecifics and less time searching for prey (Hassell 1971). However, prey consumption was not uniformly affected across host plants due to interactions between plant and predator interference. For example, at the highest predator density the area of discovery was reduced by four, 10, and 13% on castor bean, cucumber, and common bean, respectively. The large reduction in area of discovery on common bean reflects greater predator interference and a higher baseline rate of consumption on this plant, explaining the interaction between host plant and predator density. In contrast, the slower decline in searching efficiency on castor bean, independent of predator density, reflects lower predator interference as function of host plant. Thus, predator interference affects the stability of predator-prey interactions; the greater the value of the mutual interference constant, the greater the stability conferred to predator-prey dynamics (Beddington 1975). The highest area of discovery on common bean is likely attributable, at least in part, to the low density of trichomes on *P. vulgaris* leaves (Mahr et al. 2001) and a leaf surface generally amenable to foraging. In contrast, the lower consumption rates and reduced mutual interference among predators on the other plant species may be attributable to the high density of trichomes in the case of cucumber leaves (e.g., Stavrinides and Skirvin 2003), and the thick wax layers present on castor bean leaves (e.g., Eigenbrode et al. 1996), respectively. Vermeer et al. (2003) estimated that castor bean leaves contain 1.8 µg per cm^2 of epicuticular wax. Differences in plant chemistry may have subtle influences on searching behaviour, either directly through toxic or repellent effects (Vet and Dicke 1992), via defensive compounds induced by herbivore feeding, or via indirect effects on the palatability of the prey (Sabelis et al. 1999). Thus, contributions of leaf chemistry to host plant effects in the present study cannot be ruled out, although there do not appear to be any reports of phytochemistry directly affecting

coccinellid searching efficiency (Hodek and Evans, 2011). It seems more likely that the surface structures of cucumber and castor bean leaves mechanically impeded the movement of *S. gilvifrons* and/or decreased the reactive distance to prey.

Our results suggest that the physical features of the plant surface can affect the predation rate of *S. gilvifrons* but not the type of functional response, which remained type II on all three plant species. These observations are consistent with observations of *S. gilvifrons* foraging on European red mite, *Panonychus ulmi* (Koch) (Haji-Zadeh et al. 1994), date dust mite, *Olygonychus afrasiaticus* McGregor (Matin 2008), sugarcane mite, *Oligonychus sacchari* (McGregor) (Afshari 1999) and citrus brown mite, *Eutetranychus orientalis* (Klein) (Imani and Shishehbor 2011). However, type I and II functional responses have been reported for other *Stethorus* spp. foraging in other contexts (Gotoh et al. 2004, Biddinger et al. 2009).

Our estimates of straight and hooked trichome densities on the abaxial surface of common bean leaves were similar to those reported by Riddick and Wu (2011) for Lima bean, *Phaseolus lunatus* L. (Henderson cultivar). Effects of leaf surface microstructures (e.g., hairs, glandular trichomes, and domatia) on plant mites and their predators have been well studied (e.g., Chien and Sussex 1996, Krips et al. 1999, Loughner et al. 2008, Sudo and Osakabe 2011), but possible differences between upper versus lower leaf surfaces were usually ignored. Many plant-dwelling mites occur preferentially on abaxial leaf surfaces (Sudo and Osakabe 2011) and yet hairs and/or trichomes that obstruct predator foraging (Krips et al. 1999, Loughner et al. 2008) are generally denser on abaxial than on adaxial surfaces and the former tend to have more stellate hairs than the latter (Chien and Sussex 1996).

Direct comparisons of attack rates and handling times among studies are difficult because experimental conditions vary (plants, prey species, observational setting, etc). However, the maximum predation rate for *S. gilvifrons* on these host plants (44–59 adult mites / beetle / day) is somewhat higher than that recorded on *Oligonychus afrasiaticus* McGregor provided on date palm shoots (Latifian 2012). Although the nature of the functional response remained invariant across host plants, searching efficiencies were highest and handling times, lowest, on common bean. Similarly, the maximum number of prey attacked, given by the asymptote (T / T_h) of the response curve, was greatest on common bean. Adult *S. gilvifrons* were more efficient predators of *T. urticae* adults on common bean

than on castor bean or cucumber due to a > 40 % reduction in handling time on the former plant. The long handling times on cucumber and castor bean are likely due to the high density of hooked trichomes on the former, and thick leaf surface waxes on the latter. Similarly, differences in functional response parameters of *P. persimilis* to spider mites among different plants have been attributed to differences in trichome density and other morphological characters (Skirvin and Fenlon 2001).

Predator foraging efficiency may be decreased on waxy surfaces because predators are more inclined to slip from leaves or engage in activities other than searching for prey. Eigenbrode et al. (1996) suggested that the thick layer of wax on the underside of castor bean leaves reduced the foraging efficiency of predators on this plant. *Picromerus bidens* (L.) (Pentatomidae, Hemiptera) captured fewer prey on tomatoes than on sweet pepper or eggplant due to longer handling times on tomato leaves that possess hooked trichomes (Mahdian et al. 2007). Experimental releases of *S. punctillum* to suppress *T. urticae* in greenhouses resulted in establishment and pest suppression on pepper and cucumber plants, but not on tomato plants, again due to leaf trichomes (Raworth 2001). In contrast, Rott and Ponsonby (2000) found that performance of *S. punctillum* searching for *T. urticae* was best on tomato, but cultivars different from the former study were employed.

Our results suggest that host plant effects on the functional response of *S. gilvifrons* become more apparent at higher prey densities, much as observed for *P. persimilis* (Skirvin and Fenlon 2001). However, differences in prey consumption at lower prey densities may require longer experimental periods to detect. Moreover, predators may become less willing to struggle against plant impediments as they become satiated. For example, Walters (1974) found that the hooked trichomes on *P. lunatus* and *P. vulgaris* leaves lacerated and penetrated the integument of abdominal segments of three *Stethorus* spp. larvae, causing significant mortality, and also caused injury to adults. Riddick and Wu (2011) reported that larvae, but not adults of *S. punctillum* nor adult *T. urticae*, were impaled or entrapped by trichomes on the abaxial surfaces of *P. vulgaris* (lima bean) leaves, whereas Kavousi et al. (2009) showed that *P. vulgaris* hooked trichomes occasionally trapped and killed adult *T. urticae*.

These laboratory experiments offered a single life stage of prey confined in a small arena and may not accurately predict predator performance in a greenhouse or field population with all life stages distributed in patches over larger spatial scales; follow-up

studies could validate these results by comparing predator-prey ratios among these plants under open field conditions. Nevertheless, the effectiveness of naturally-occurring *S. gilvifrons* against *T. urticae* in Egyptian vegetable crops, either alone or in conjunction with predatory mites, can be expected to vary as a function of leaf surface properties. We conclude that biocontrol efficacy will be enhanced on crops with relatively smooth leaves, and diminished on those with waxy leaves or high densities of trichomes.

Acknowledgments

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Fig. 1. Changes in mean ± SE total number of prey consumed as a function of number of beetles foraging (A) and killing power (B), the latter derived from the difference between the logarithms of the mite population before and after a 12 h period of predation by female *Stethorus gilvifrons* foraging for *Tetranychus urticae* (80 adult mites) at various predator densities on 6.0 cm^2 leaf discs of each of three host plants (solid line, castor bean; dashed line, common bean; hatched line, cucumber).
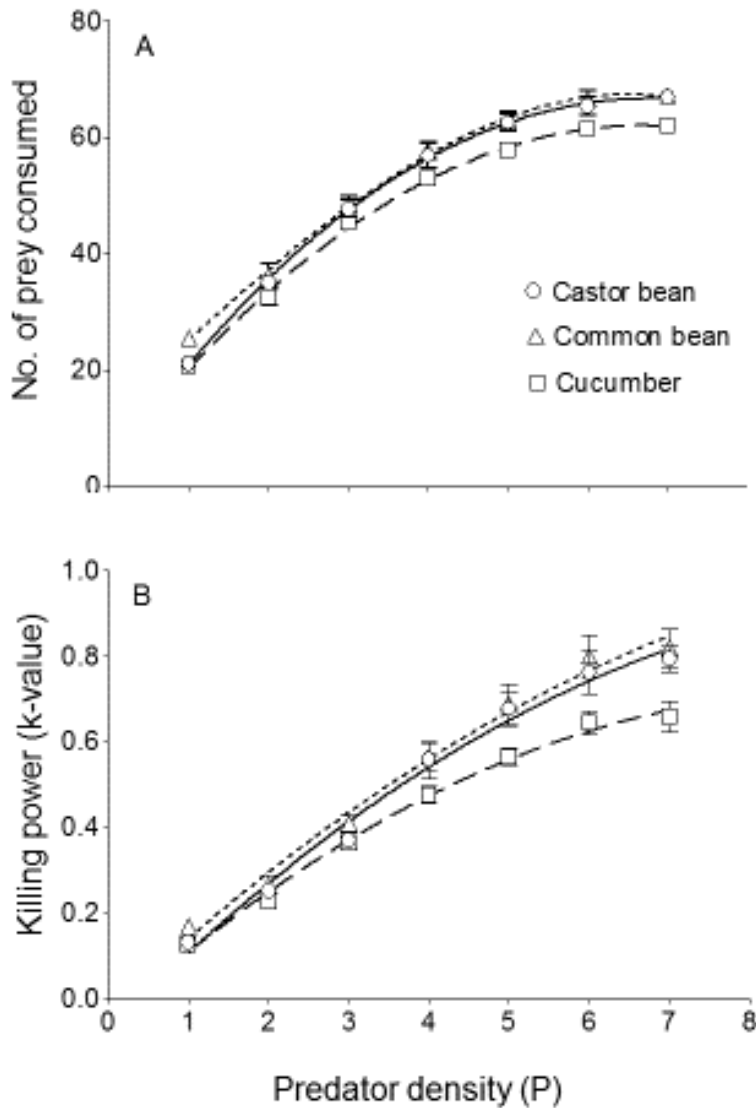
Fig. 2. Changes in mean ± SE area of discovery for female *Stethorus gilvifrons* during a 12 h period of foraging for *Tetranychus urticae* (80 adult mites) on 6.0 cm^2 diameter leaf discs of three different host plants (solid line, castor bean; dashed line, common bean; hatched line, cucumber) as a function of increasing predator density.
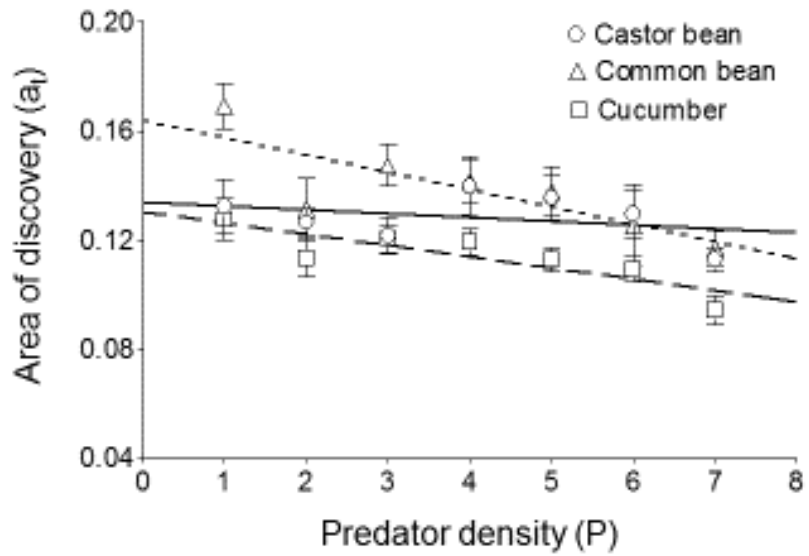
Fig. 3. Changes in mean ± SE interference levels derived from the relationship between logarithm of predator density (P) and area of discovery (a_t) for female *Stethorus gilvifrons* during a 12 h period of foraging for *Tetranychus urticae* (80 adult mites) on 6.0 cm^2 diameter leaf discs of castor bean (solid line, $\log a_t = -0.88 - 0.03 \log P$, $F_{1,68} = 0.58$, ns), common bean (dashed line, $\log a_t = -0.79 - 0.131 \log P$, $F_{1,68} = 11.76$, $P < 0.05$), and cucumber (hatched line, $\log a_t = -0.89 - 0.104 \log P$, $F_{1,68} = 11.14$, $P < 0.05$).
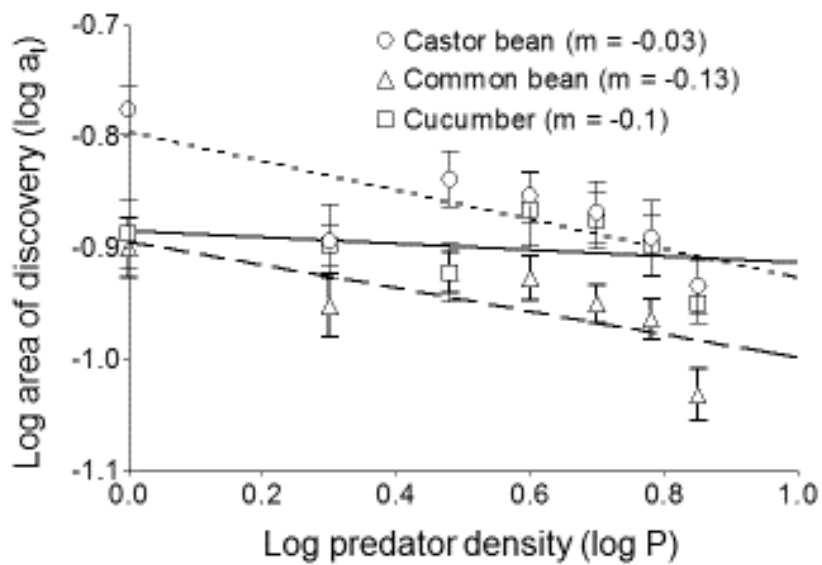
Fig. 4. Changes in mean ± SE numbers of adult *Tetranychus urticae* consumed by female *Stethorus gilvifrons* (A) and the proportion consumed (B) as a function of increasing prey density. Beetles were offered mites on 6.0 cm^2 diameter leaf discs of three different host plants (solid line, castor bean; dashed line, common bean; hatched line, cucumber). Lines represent the best-fit type II functional response curves (A) and logistic regression models (B).
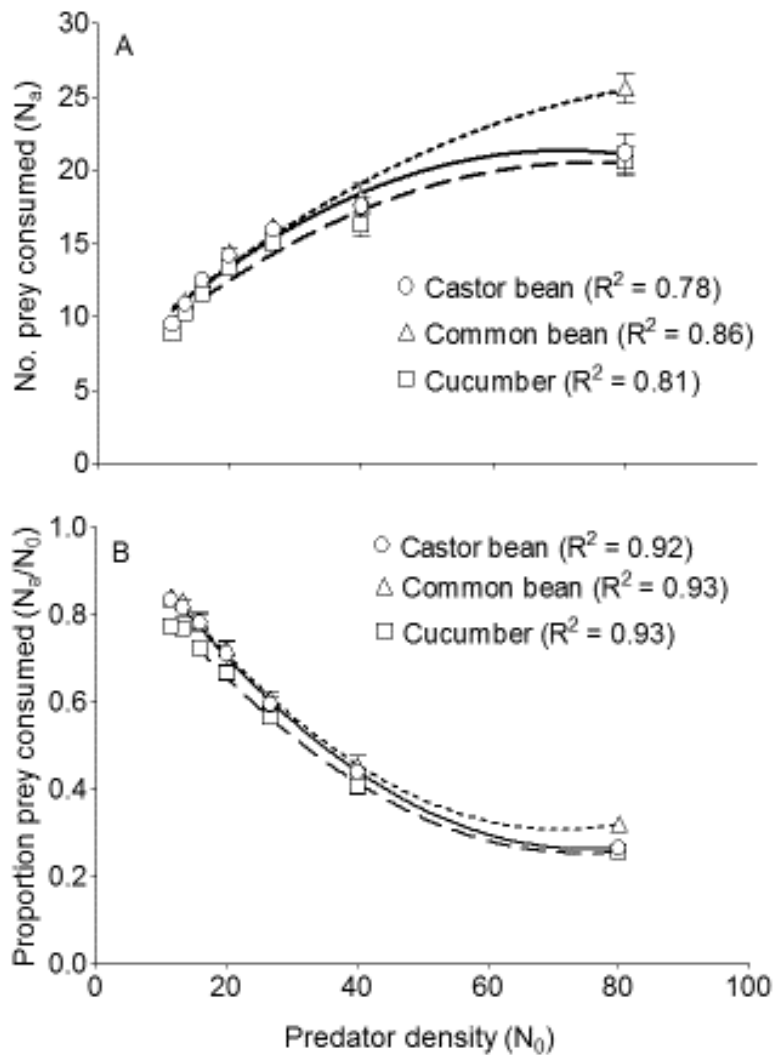
Table 1. Mean ± SE prey consumption by individual female *Stethorus gilvifrons* at various predator densities during a 12 h period foraging for 80 adults of *Tetranychus urticae* on a 6.0 cm^2 leaf disc of one of three plant species.

Predator density	No. prey consumed / predator (n = 10)			F	df	p
	Castor bean	Common bean	Cucumber			
1	21.20 ± 3.92Ba	25.60 ± 3.07Aa	20.60 ± 3.01Ba	5.94	2,27	< 0.05
2	17.55 ± 1.65Ab	17.85 ± 2.95Ab	16.25 ± 2.19Ab	1.17	2,27	> 0.05
3	15.93 ± 1.48Abc	16.17 ± 1.47Ac	15.10 ± 1.19Ab	1.47	2,27	> 0.05
4	14.22 ± 1.62Acd	14.45 ± 1.09Ac	13.25 ± 0.96Ac	2.32	2,27	> 0.05
5	12.62 ± 0.92Ade	12.58 ± 0.99Ad	11.58 ± 0.68Bd	3.71	2,27	< 0.05
6	10.90 ± 0.78Aef	11.12 ± 0.68Ae	10.15 ± 0.58Bde	3.93	2,27	< 0.05
7	9.26 ± 0.42Af	9.60 ± 0.53Ae	8.86 ± 0.55Be	6.16	2,27	< 0.05
F	35.79	77.18	56.63			
df	6,63	6,63	6,63			
p	< 0.001	< 0.001	< 0.001			

Means followed by different upper case letters were significantly different within rows, and those followed by different lower case letters, within columns (Bonferroni, $\alpha = 0.05$).

Table 2. Maximum likelihood estimates obtained from logistic regression of the proportion of adult *Tetranychus urticae* consumed by adult females of *Stethorus gilvifrons* as a function of initial prey density on different leaf types.

Host plant	Parameter	Estimate	SE	df	X^2	P
Castor bean	Intercept (P_0)	2.62	0.24	1	121.9	< 0.001
	Linear (P_1)	-0.099	0.012	1	65.46	< 0.001
	Quadratic (P_2)	0.00067	0.00012	1	30.71	< 0.001
Common bean	Intercept (P_0)	2.489	0.231	1	115.94	< 0.001
	Linear (P_1)	-0.0941	0.012	1	61.65	< 0.001
	Quadratic (P_2)	0.00067	0.00012	1	32.15	< 0.001
Cucumber	Intercept (P_0)	2.292	0.2262	1	102.63	< 0.001
	Linear (P_1)	-0.094	0.0119	1	62.26	< 0.001
	Quadratic (P_2)	0.00065	0.00012	1	30.24	< 0.001

Table 3. Mean attack rate (a), handling time (T_h), and 95% confidence intervals (CI) for adult females of *Stethorus gilvifrons* searching on *Tetranychus urticae* adults on different leaf types.

Host plant	Attack rate (a)	SE	Asymptotic 95% CI Lower	Upper	Handling time (T_h)	SE	Asymptotic 95% CI Lower	Upper
Castor bean	0.1922b	0.0270	0.1579	0.2264	0.52a	0.0190	0.4842	0.5610
Common bean	0.2543a	0.0171	0.1999	0.3088	0.41b	0.0172	0.3787	0.4471
Cucumber	0.2082b	0.0197	0.1689	0.2475	0.54a	0.0196	0.4985	0.5769

Means bearing different letters were significantly different from others in the same column (Bonferroni, $\alpha = 0.05$).

Table 4. Comparative morphology of leaves. All measurements are mean ± SE (n = 10). Trichomes were counted on abaxial surfaces.

Plant	Venation	Trichome type	Leaf tissue thickness (µm)			Trichome density (no. / cm^2)		Trichome length (µm)	
			Blade	Palisade	Spongy	Straight	Hooked	Straight	Hooked
Castor bean	pinnate	none	3200 ± 18a	400 ± 8a	280 ± 9a	–	–	–	–
Common bean	palmate	hooked	2000 ± 14b	90 ± 6c	80 ± 4c	–	6 ± 1b	415 ± 9b	–
Cucumber	palmate	hooked and straight	1100 ± 23b	140 ± 4b	125 ± 5b	11 ± 2	27 ± 3a	550 ± 7a	110 ± 7
df			2, 27	2, 27	2, 27		2, 18	2, 18	
F			28010	5834	2238		38.79	1254.01	–
p			< 0.001	< 0.001	< 0.001		< 0.001	< 0.001	–

Means bearing different letters were significantly different from others within a column (Bonferroni, $\alpha = 0.05$).