

Time allocation of *Orius sauteri* in attacking *Thrips palmi* on an eggplant leaf

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Abstract

Orius sauteri (Poppius) (Heteroptera: Anthocoridae) is a polyphagous predator used as a biological control agent of palm thrips, *Thrips palmi* (Karny) (Thysanoptera: Thripidae). We studied *O. sauteri*'s searching efficiency, time allocation on a leaf, leaving tendency, and attacking of prey. Approximately 78% of the encountered prey was eaten. Searching for prey was concentrated for 86% of the time on the lower leaf side, where palm thrips are usually found. Patch residence times on empty leaves were different from those on leaves with *T. palmi* larvae. Walking activity was not affected by the thrips density, and walking took place during 64% of the total search time. The leaving tendency of *O. sauteri* was affected by the time from patch entry and the presence or absence of palm thrips, but not by the thrips density. If prey were present, the leaving tendency decreased (multiplication factor 0.327), resulting in longer giving-up times than when no prey was present. The fact that the leaving tendency increases when patch exploitation lasts longer suggests that not much time is wasted on patches where encounters with prey are scarce.

Introduction

Augmentative biological control with arthropod natural enemies is very common throughout the world and has become an effective method of pest control in integrated pest management (IPM) in greenhouse crops (e.g., Albajes et al., 1999). Anthocorid bugs, *Orius* spp., are important generalist predators used to control thrips in greenhouses (Castañé et al., 1999). Yasunaga (1997a,b,c) recorded seven Japanese *Orius* spp., of which four, viz., *Orius sauteri* (Poppius) (Heteroptera: Anthocoridae), *Orius strigicollis* (Poppius), *Orius minutus* (L.), and *Orius tantillus* (Motschulsky), are considered important predatory bugs of *Thrips palmi* (Karny) (Thysanoptera: Thripidae), a serious pest to fruit vegetables (Kawai, 1990; Walker, 1994) in the field. As the suppressive effect of *O. sauteri* on *T. palmi* infesting

eggplants has been demonstrated in the field and in greenhouses (Kawai, 1995; Nagai, 1996), it has been registered as a biological control agent for commercial use in greenhouses since 1998.

Evaluation of natural enemies is the most critical phase in the development of biological control programmes in greenhouses (van Lenteren & Manzaroli, 1999). Moreover, searching efficiency is an important parameter to be evaluated in the assessment of classical biological control agents (Huffaker et al., 1976). The effect of searching efficiency on biological control should be evaluated at the population level. Therefore, patch exploitation behaviour by individuals is an essential factor, and models provide an effective tool to link patch exploitation behaviour and biological control. *Phytoseiulus persimilis* (Athias-Henriot) (Acari: Phytoseiidae) and *Encarsia formosa* (Gahan) (Hymenoptera: Aphelinidae) are two classical natural enemies used for augmentative biological control in greenhouses. Sabelis (1981) and Sabelis & van Rijn (1997) have developed models to describe patch exploitation

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behaviour and have discussed the implications of the predation rate and the predators' behaviour on the biological control of spider mites with *P. persimilis*. A detailed simulation model has been developed to link patch exploitation behaviour of *E. formosa* and the population dynamics of *E. formosa* and the greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood) (Homoptera: Aleyrodidae) (van Roermund et al., 1994, 1997; van Roermund & van Lenteren, 1995a). From sensitivity analysis of the model, they concluded that the patch residence time and the host handling time have large effects on the host density.

Orius sauteri is registered as a biocontrol agent and has already been evaluated with respect to prey selection, reproduction, and predation capability (Nagai & Yano, 1999, 2000). To improve biocontrol with *O. sauteri* and other *Orius* species, its prey-searching within a patch (an eggplant leaf) has been studied. The results of this study will be used as input to develop a model of functional response by *O. sauteri* in the heterogeneous environment of a greenhouse. The effect of parameters describing *O. sauteri*'s foraging behaviour on biological control can be evaluated at the population level with such a model.

In this study, we investigated *O. sauteri*'s handling time of prey, ratio of successful attack, fraction of time it spends on the lower leaf side where prey is available, residence times on eggplant leaves, walking activity, and response to various prey densities. The handling time and the patch residence time are essential factors limiting the overall predation rate of *Orius* in the patch. The ratio of successful attack is directly related to the predation rate in each encounter. The fraction of time that *Orius* spends on the lower leaf side is necessary for determining the searching area of *Orius*. The walking activity, i.e., the proportion of walking time of the total for walking and resting time in a patch until patch leaving, is an important parameter that determines the foraging speed in a patch. The response of predators to different prey densities is studied, because predators forage in heterogeneous (greenhouse) environments. Moreover, we are the first to assess how factors influence the leaving tendency of a predator, based on realized or censored giving up times (GUTs), on an eggplant leaf, i.e., the probability per unit time of leaving such a leaf. We test whether the leaving tendency is affected by the absolute number of thrips in a patch or by the number of prey that are rejected or eaten. During the exploitation of the eggplant leaf, the leaving tendency can change and this was investigated by including the time from patch entry, i.e., the time that the bug is already searching in the current patch, as a factor in the proportional hazards model.

Materials and methods

Plants and insects

Clean potted eggplants (*Solanum melongena* L. cv. Senryo) were grown in a clean glasshouse compartment (25 ± 2 °C, r.h. was not controlled). The plants used for observation trials were about 30 cm high. A leaf with an area of approximately 100 cm² was selected for each trial. Kidney beans (*Phaseolus vulgaris* L. cv. Hatsumidori) were used for rearing *T. palmi*, derived from the Okayama Prefectural Agricultural Experiment Station, in a greenhouse compartment (25 ± 2 °C, r.h. was not controlled).

A laboratory culture of *O. sauteri* was started in June 1993 with adults collected from white clover in the field of Okayama Prefectural Agricultural Experiment Station in San'yo-cho, Japan. Stock cultures have been maintained in the laboratory at 25 ± 1 °C and L16:D8. Both nymphs and adults were fed with *Ephestia kuehniella* (Zeller) eggs. The strain of *E. kuehniella* was started in 1992 with individuals from a culture maintained at the National Food Research Institute in Tsukuba, Japan. Soybean sprouts were provided to female adults as oviposition substrates (Zhou et al., 1991).

Experimental set-up

We observed the searching behaviour of *O. sauteri* on an eggplant leaf with a varying number of *T. palmi* prey in glasshouse experiments to study time allocation on a leaf, leaving tendency, and attack on prey. Observations were carried out in a heated glasshouse with an area of 16 m² during the daytime (09:00–15:00 hours). Temperature in the glasshouse was maintained at 25 ± 3 °C by ventilation. One day prior to trials, five 7-day-old female *O. sauteri* individuals were placed in a plastic container (diameter 9 cm × height 6 cm). They were fed with ample 2nd instar larvae of *T. palmi* (30 prey individuals per predator) on an eggplant leaf covering the entire bottom of each container and kept until the onset of the trials.

One day before each trial, a fixed number of the 2nd instar *T. palmi* larvae were detached from the leaf in the container and inoculated on the lower side of an eggplant leaf. Because *T. palmi* larvae are mobile, the number on the lower side had to be adjusted, and the larvae on the upper leaf side were removed just before the start of the trial. The treatments were different with respect to the density of *T. palmi*, either 0, 1, 5, 10, or 20 per eggplant leaf. For each of these five treatments, 16–19 replicates were performed. Kawai (1995) carried out release experiments of *O. sauteri* to control *T. palmi* on greenhouse eggplants. The thrips density became stabilized around EIL (0.55 individuals per leaf). Although *T. palmi* has an aggregated distribution among leaves, 0–20 individuals per leaf in our study reflects a realistic density of *T. palmi* on greenhouse eggplants.

To start a trial, one female *O. sauteri* was released near the petiole of the lower leaf side of a potted eggplant leaf. The behaviour of *O. sauteri* was observed by the naked eye and recorded using the computer software package THE OBSERVER (Noldus Information Technology, 1996). The observation was stopped when *O. sauteri* left the leaf, either by walking (and was off patch for at least 1 min) or by flight. The behavioural components recorded during observation were (a) walking, (b) resting (standing still), (c) eating a prey (thus measuring handling time for predation), and (d) passing a prey, a sort of rejection of the prey, because the bug keeps on walking immediately after touching the prey with its legs. Throughout the trials, the position of *O. sauteri* on the leaf was recorded: the upper leaf side, the lower leaf side, and the petiole.

Survival analysis

Here we give a short explanation of the proportional hazards model. For a more thorough description we refer to Kalbfleisch & Prentice (1980) and Haccou & Hemerik (1985). The proportional hazards model is used to analyse which experiences of a predator are correlated to an increase or decrease in the tendency of the predator to leave a prey patch. It is assumed that the predators have a basic tendency to leave the patch (baseline hazard), which is reset after certain events. These are called renewal points and occur in our analysis at the moment a patch is entered and when searching is resumed after the consumption of a prey. The choice of such renewal points implies that the statistical analysis is performed on GUTs (real and censored bouts) and all covariates could be treated as fixed. The effects of the chosen factors on the leaving tendency are given in the following equation:

$$h(t; z) = h_0(t) \exp\left(\sum_{i=1}^n \beta_i z_i\right)$$

where $h(t; z)$ is the probability per second of leaving the patch (in our case, when the predator walks or flies from the leaf) at time t with the vector of covariate values $z = (z_1, \dots, z_n)$, and $h_0(t)$ is the basic tendency to leave, i.e., when there is no effect of any experience on the patch. The z_i are the fixed factors (covariates) that might influence the leaving tendency. Each factor z_i can attain different values. The β_i values represent the relative strengths of the effects of the covariates. For this model, the relative strengths of each of n covariates is estimated together with the baseline hazard by means of partial likelihood maximization (see Kalbfleisch & Prentice, 1980). The influence of experiences (the covariates) on the leaving tendency is modelled as a multiplicative effect on the baseline hazard by $\exp(\beta_i z_i)$. If this term is below 1, the

leaving tendency is reduced, above 1, it is increased. An increased leaving tendency corresponds to a shorter GUT. If the cumulative baseline hazard in time is nearly a straight line, the expected GUT can be approximated by $1 h^{-1}(t; z)$. The factors of interest for *O. sauteri* were taken as the number of thrips it passed, the number of thrips it ate, the number of thrips in the patch, and the time from patch entry at the most recent renewal point.

For the analysis of patch residence times at different prey densities, we used the log-rank test (Kleinbaum, 1996), because some of the residence times were censored. The analyses with techniques from survival analysis were performed in SPSS 11.0 (SPSS, 2001).

Other statistics used

For determining the effect of the initial number of thrips and the predator individual, we performed an analysis of variance on the handling times. We used logistic regression analysis to determine whether the individual predators have significantly different attack rates. Linear regression was performed on the arcsine-transformed walking activity and percentage of time spent on lower leaf side to determine whether this depended on the initial number of thrips. We applied a generalized linear model (GLM) to analyze the effect of the number of thrips on a leaf on the predation rate and on the number of prey eaten. In the GLM analysis, it was assumed that the predation rate and the number of prey eaten follow a Binomial distribution and a Poisson distribution, respectively. For GLM, SAS 8.02 (SAS Institute, 1999) was used. All other statistical analyses were performed in JMP 5.01 (SAS Institute, 2002).

Results

Summary of behavioural characteristics

The overall mean of the handling time for predation of a single thrips larva was 199.8 ± 11.5 s (sample mean \pm SE; $n = 164$). Analysis of variance showed no significant effects on the handling times, neither of the initial thrips number ($F = 1.08$, d.f. = 3, $P = 0.359$) nor of the predator individual ($F = 1.14$, d.f. = 40, $P = 0.249$). When a predator encountered a thrips larva, it attacked and ate the larva in most cases. The mean ratio of a successful attack to an encounter was 0.774 ± 0.029 (sample mean \pm SE; $n = 212$). Logistic regression analysis resulted in a significant effect of the predator individual on the attack rate ($\chi^2 = 59.68$, d.f. = 42, $P = 0.038$). The behaviour of prey passing was almost instantaneous, with no handling time. *Orius sauteri* searched on the lower side of a leaf most of the time. The percentage of time spent on the lower leaf side was affected neither by the presence of thrips nor by the number of

Table 1 Mean percentage of time spent on the lower leaf side of eggplants by *Orius sauteri* when a different number of thrips larvae are infested on a leaf (n denotes the sample size, and values in parentheses are SE). The lower row gives the median values for the total residence time (s)

Parameters	Initial number of thrips (nr)				
	n nr = 0	n nr = 1	n nr = 5	n nr = 10	n nr = 20
Percentage of time on lower leaf side	17 77.3 (6.1)	19 80.2 (5.5)	18 90.9 (2.7)	18 91.3 (2.5)	16 92.5 (9.8) *
Residence time (s)	17 467 a	19 1878 b	18 1599 b	18 1907 b	16 1800 b **

*One-way ANOVA, after applying the arcsine transformation, $F = 2.03$, d.f. = 4, $P = 0.109$.

**Pairwise log-rank test with Bonferroni correction because 5% of residence times were censored. Different letters within a row indicate significant differences.

thrips larvae introduced (Table 1). The overall mean of this percentage was $86.3 \pm 1.9\%$ (sample mean \pm SE; $n = 88$). The residence time of *O. sauteri* on a leaf (excluding the prey handling time) was shorter on a leaf without thrips than the one with thrips, and using the log-rank test (Kleinbaum, 1996) the difference between a leaf without thrips and with thrips was always statistically significant, irrespective of the prey density (Table 1). Moreover, we computed the walking activity as the time that a predator walked divided by the total time for walking and resting in the patch. This proportion did not differ with the initial number of thrips in the patch; the regression of the arcsine transformed walking activity on the initial number of thrips was not significant ($F = 3.07$, d.f. = 86, $P = 0.0832$). The overall mean of the walking activity was 0.644.

Predatory response

For an estimate of the predatory response of *O. sauteri* to the number of *T. palmi*, we plotted the predation rate from the start of observation until the predator leaves the patch and the number of prey eaten against this initial prey number (Figure 1). The predation rate showed a unimodal curve and the number of prey eaten showed a sigmoidal response. The predation rate was highest at an initial prey number of five or 10. Because the total residence time in trials with different initial densities of prey was not statistically different (Table 1), Figure 1 can be considered as a functional response. The GLM analysis showed that the number of thrips on a leaf significantly affected both the predation rate ($\chi^2 = 100.98$, d.f. = 3, $P < 0.0001$) and the number of prey eaten ($\chi^2 = 15.52$, d.f. = 3, $P = 0.0014$).

Leaving tendency

For the analysis using the proportional hazards model, we first plotted the cumulative hazard function for different values of the tested covariates. Figure 2A shows how the leaving tendency of *O. sauteri* is affected by the presence of

thrips. The reaction of *O. sauteri* is, however, not different (log-rank test, in all pairwise comparisons $P > 0.24$) when different numbers of thrips are present, and all were significantly different from the treatment without thrips (all three pairwise comparisons $P < 0.06$). Therefore, we subsequently redefined the covariate 'number of thrips present' as 'prey absent or present' (Figure 2B), giving us the result of significantly different leaving tendencies in the proportional hazards model. For the covariates 'number of prey eaten' and 'number of prey passed', a similar inspection was conducted; the log-rank test for all pairwise comparisons of (≤ 8) prey eaten resulted in $P > 0.24$ and thus no difference, whereas all pairwise comparisons for prey passed showed no difference too ($P > 0.23$). The results of the log-rank test convinced us that we did not have to include these covariates in the

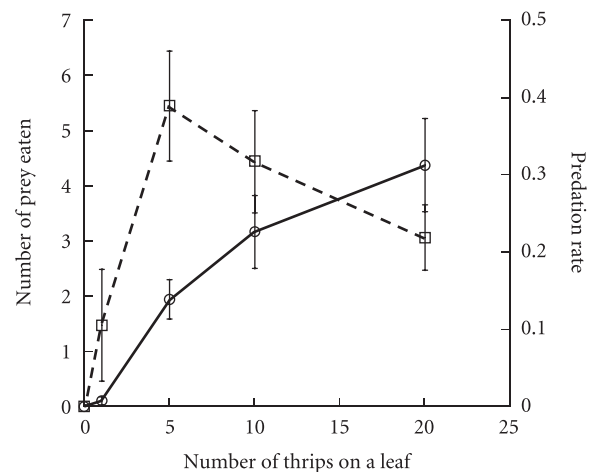


Figure 1 The predation rate (dashed line) and the number of thrips eaten (solid line) by *Orius sauteri*, plotted against the initial number of thrips. Vertical bars indicate SE.

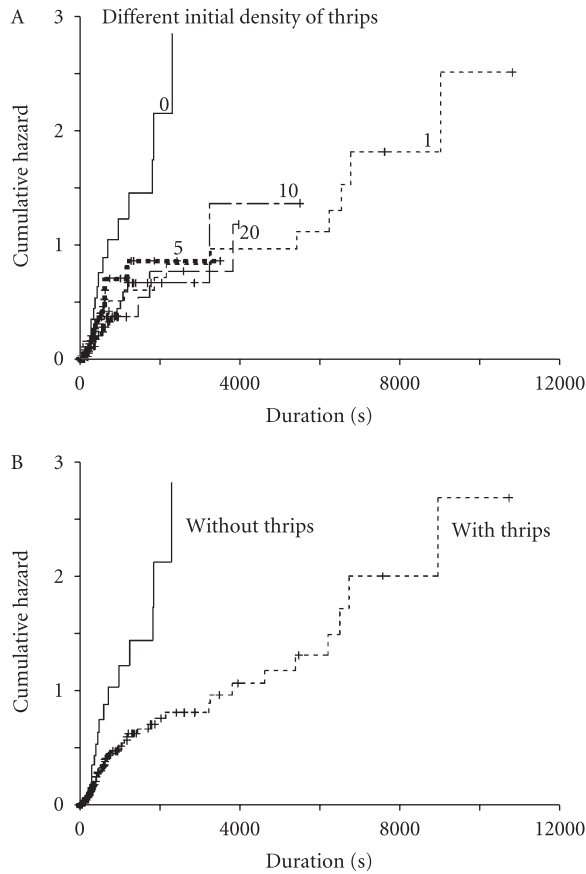


Figure 2 Cumulative leaving tendency of *Orius sauteri* (A) in patches with different initial numbers of thrips and (B) when density is scored as prey absent or present. A plus sign (+) indicates a censored observation.

proportional hazards analysis. From the resulting model with two covariates the effects were estimated, and we summarize the results in Table 2. Both the presence and absence of thrips and the time from patch entry (in min) at the start of the current GUT determined the leaving behaviour of *O. sauteri*. When the predator has been searching in the patch for 10 min, and it has not left, its leaving tendency is already $1.013^{10} = 1.14$ times higher

than when it just started searching for prey in the current patch. Because both these factors occur independently, the leaving tendency is reset to its original level on an empty leaf when a renewal point occurs at about 100 min on a leaf with thrips [$0.277 * (1.013)^{100} \approx 1$].

Discussion

Orius sauteri adult females spend most of the time on the lower leaf side and attack the majority of the prey, i.e., thrips larvae, upon encounter. It is advantageous to search on the lower leaf side because under natural conditions this is where most prey are to be found. Several other predators and parasitoids are known to prefer the lower side of the leaf, e.g., *Orius tristicolor* (Shields & Watson, 1980) and *Encarsia formosa* (van Roermund & van Lenteren, 1995b).

Orius sauteri is a generalist predator used in controlling thrips in greenhouses. This type of predator is released when pest populations have reached high densities (Brodeur et al., 2002). *Thrips palmi* has an aggregated distribution among leaves, and must have reached high densities in hot spots when *O. sauteri* is released. Soon after its release, *O. sauteri* is expected to be satiated, yet it still has to perform its task as a biological control agent. With this in mind, it is reasonable to use satiated predators in experiments. In addition, the hunger levels of the predators used in our experiments was easily standardized. Although *O. sauteri* females used in the trials were satiated, they attacked the majority of encountered thrips larvae. Moreover, the predation rate was independent of the initial thrips density. Satiated adults still showed a high tendency to attack independently of their experience of predation during trials. It is very different from the cases of predatory mites where attack tendency is strongly affected by the starvation level of the predator (e.g., Fransz, 1974; Rabbinge, 1976; Sabelis, 1981). One possible explanation for the high attack tendency of satiated *O. sauteri* adult female is that the attack tendency is not regulated by hunger. This is illustrated by the fact that when excessive numbers of thrips are always supplied to this predator in rearing experiments, it frequently kills thrips individuals by stinging without

Table 2 The effects on the leaving tendencies estimated with the proportional hazards model from behavioural records on *Orius sauteri* by analysing observed and censored GUTs. The significance threshold for the χ^2 distribution with 2 d.f. is 5.99 at the 0.05 level

Covariates	Effect exp (β)	Wald statistic	Significance P-value
Are prey present in the patch? (1/0 = yes/no)	0.277	15.797	<0.001
How long ago (in min) was the patch entered at the latest renewal point?	1.013	8.885	<0.02

fully sucking prey fluids (Nagai, unpubl.). Whether starved *Orius* have higher attack tendencies remains to be investigated.

The total residence times in trials with different initial densities of prey were not statistically different (Table 1). Therefore, Figure 1 can be considered as a functional response. *Orius sauteri* showed a Holling type-III response, considering the change of predation rate in Figure 1 (Holling, 1965; van Alphen & Jervis, 1996). This can be explained if the predator becomes increasingly efficient at finding prey as prey density rises (Hassell, 2000). Both thrips and *Orius* adults show thigmotactic behaviour (Nagai et al., 1988; Chambers et al., 1993), which leads to both species being present along the leaf veins of lower leaves. *Orius* species are known to be attracted to a cucumber leaf with thrips or spider mites (Venzon et al., 1999). Female *O. sauteri* might be attracted to the leaf parts damaged by thrips. These are the possible mechanisms for explaining *O. sauteri*'s high searching efficiency for thrips larvae on a leaf.

Although *O. sauteri* searched prey thrips efficiently on a leaf, it exploited each patch only partially. The main reason for partial exploitation in a patch is the very short distance of perception of the bug. It could not recognize a prey item at a distance of a few millimetres. It recognized a prey only when it touched it with its legs during its search. In addition, thrips individuals are distributed sparsely on a leaf without forming colonies like aphids or spider mites. The bug rejected some prey individuals during patch exploitation, but this rejection was very different from the rejection behaviour of parasitoids. It kept on walking after touching the prey with its legs without handling. It is likely that the bug simply did not recognize these prey individuals.

The leaving tendency of *O. sauteri* from a leaf patch was affected by the time from patch entry at the start of the current GUT, and the presence or absence of thrips larvae, but apparently not by their initial density. The most likely mechanism is the response of *Orius* to chemical cues from the leaf with thrips. In greenhouse release–recapture experiments, *Orius laevigatus* showed a significant preference for plants infested by *Frankliniella occidentalis* rather than clean plants (Venzon et al., 1999). *Orius sauteri* has been shown to be attracted to bean leaves damaged by *T. palmi* and not to discriminate between different numbers of thrips in Y-tube olfactometer experiments (Mochizuki, unpubl.). These results are in accordance with the results of the present study. Leaving tendency increases with the time from patch entry, meaning that as long as no prey is encountered, the predator is more eager to leave as time goes by. This is considered to be advantageous because empty leaves or leaves with low densities provide no or fewer opportunities to encounter prey, and thus, it

seems better for the predator to leave when no prey has been encountered after some time.

Recent studies of how parasitoids acquire information and allocate their time to the exploitation of host patches use a combination of functional and causal approaches. The presence and concentration of kairomones can provide information to the parasitoid about the patch size and host density (Galis & van Alphen, 1981). Patch exploitation by parasitoids is modulated by the different experiences whilst foraging. Ovipositions can increase or decrease patch-residence time (Waage, 1979; Driessen & Bernstein, 1999). The kind of mechanism that parasitoids use depends on the distribution of hosts and the travel times between patches under field conditions. Marking pheromone concentrations left by parasitoids and encounters with other parasitoids also affect patch time (van Alphen et al., 2003).

By contrast, the leaving tendency of the predator *O. sauteri* from a leaf might be controlled only by chemical cues from the leaf with thrips and is not affected by experiences of preying on and encountering thrips. Since *Orius* spp. are general predators which to that attack a wide range of prey species including thrips, aphids, spider mites, and lepidopteran eggs (Castañé et al., 1999). *Orius sauteri* might adopt a simple rule to find prey without depending on experiences in a patch. This should be advantageous when the range of prey species shows a great variety in behaviour or nutritional value or both, or has a random spatial distribution.

The objective of this study into the biological control of *T. palmi* with *O. sauteri* was mainly to obtain the necessary information to develop a model of functional response of *O. sauteri* in the heterogeneous greenhouse environment. Moreover, this study suggests that the behaviour of *O. sauteri* is influenced by chemical cues that are produced due to the interaction between the prey and the plant leaf. These chemical cues have an arrestment effect on the bug, in such a way that the predatory bug does not waste its time on the many empty patches in a heterogeneous environment with an aggregated prey.

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