A simulation model for the functional response of *Orius sauteri* on eggplant leaves with *Thrips palmi*: Implications for biological control

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The predation capability of the anthocorid predatory bug *Orius sauteri* (Poppius) determines its effectiveness for suppressing *Thrips palmi* Karny on greenhouse eggplants. For quantifying the daily impact of one predator on its prey, we use its patch leaving behaviour on eggplant leaves with different prey numbers and scale up to the larger spatio-temporal scale of the greenhouse and one foraging day, using literature data on the distribution of *T. palmi* over eggplant leaves. The simulation result is a type-II functional response of *O. sauteri* as function of average *T. palmi* density: around the economic injury level of *T. palmi*, *i.e.*, 0.55 individuals per leaf, *O. sauteri* can find and eat approximately 10 prey per day. The sensitivity analysis showed that the baseline leaving tendency, the presence of and the encounter rate with prey have a relatively large effect on the daily mean number of prey eaten per *O. sauteri* predator, *i.e.*, its predation capability.

Keywords: Thrips palmi, Orius sauteri, Heteroptera, Anthocoridae, Thysanoptera, Thripidae, Holling type II, functional response, behaviour

The predacious anthocorid, *Orius sauteri* (Poppius), is well known to be one of the important indigenous natural enemies of *Thrips palmi* Karny on eggplants in the field in Japan (Yano 1996). If field populations of *Orius* spp. including *O. sauteri* are conserved by using selective pesticides that do not affect *Orius* spp., then *Orius* populations suppress the outbreak of *T. palmi* on eggplants in the field (Nagai 1993, Takemoto & Ohno 1996, Ohno & Takemoto 1997). *Orius sauteri* has also been demonstrated to suppress the population of *T. palmi* around the economic injury level on eggplants in greenhouses (Kawai 1995). In 1998, *O. sauteri* was registered in Japan as a biopesticide of *T. palmi* and *Frankliniella occidentalis* (Pergande) in greenhouses. Complete reproductive diapause of *O. sauteri* is induced under a short photoperiod, and thus biological control is hampered

Proc. Neth. Entomol. Soc. Meet. - volume 21 - 2010

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(Kohno 1997, Ito & Nakata 1998). Although the usefulness of *O. sauteri* is limited to conditions with a long photoperiod, it still very effectively controls *T. palmi* on eggplants, both in greenhouses and in the field.

The effectiveness of *O. sauteri* as a biological control agent of *T. palmi* mainly depends on its reproductive capacity and its predation capability. The intrinsic rate of natural increase is generally used to indicate the reproductive capacity (Birch 1948). The intrinsic rate of the natural increase of *T. palmi* without predation is 0.102 d^{-1} (Kawai 1986) and that of *O. sauteri* fed with *T. palmi* is 0.128 d^{-1} (Nagai & Yano 1999). There are no large differences in the reproductive capacity between these two species. Thus, the effectiveness of *O. sauteri* is mainly expected to depend on its predation capability.

Experiments for determining the functional response are usually performed to measure the predation capability of one predator. Many experiments have been performed on the functional response of single *Orius* predators of different species to assess their predation capability (*e.g.*, McCaffrey & Horsburgh 1986, Isenhour *et al.* 1989, 1990, Coll & Ridgway 1995, Nagai & Yano 2000, Gitonga *et al.* 2002). As the experimental arenas in most of these studies in the laboratory were very small, homogenous spaces such as a Petri dish or a plastic vial to which the *Orius* individual was confined, the number of prey attacked in a given time period was over-estimated. In addition, the predator experienced unrealistically high prey densities compared with actual densities in greenhouses or in fields where densities are around the economic injury level. In the experiments of Nagai & Yano (2000), the lowest density of thrips that could be used was three individuals per leaf, which is about five times the economic injury level. From such experiments it is impossible to obtain a good estimate of the predation capability of one *Orius* individual during one foraging day in a greenhouse. An estimate for this daily predation capability can only be calculated from experiments in which the *Orius* female could exploit many patches.

The main question asked in this paper is what number of *T. palmi* prey an individual adult female of *O. sauteri* consumes, on average, when foraging on eggplants during 1 day. We answer this question by scaling up from our earlier findings concerning the foraging process and the patch leaving behaviour of *O. sauteri* (Yano *et al.* 2005). We have developed a simulation model in which the simulated individual encounters a realistic distribution of prey over eggplant leaves. This is assumed to be a negative binomial distribution of prey over leaves, because insects are often found to have a clumped distribution (Harcourt 1961, Atkinson & Shorrocks 1984). Data supporting this clumping for *O. sauteri* have been found in the literature from mean crowding estimations (Kawai 1986). The results from the simulation model are discussed against the background of earlier experimental findings on the functional response, *e.g.*, van Roermund *et al.* (1997).

MATERIALS AND METHODS

The structure of the simulation model

As we want to determine how many 2nd instar larvae of *T. palmi* a single female *O. sauteri* adult consumes in one foraging day, we have based our simulation model (the flowchart is given in Fig. 1) on studies where the distribution of thrips larvae is determined in greenhouses (Kawai 1986) together with the patch leaving behaviour studied by Yano *et al.* (2005) from which we have detailed estimates (see below) on how certain covariates influence the giving up time (GUT), *i.e.*, the time between patch entry and leaving if no prey is encountered, or the time between consumption of the latest encountered prey in a patch and the time the predator leaves the patch. The patch that is considered here is the eggplant leaf. The simulation model is not spatially explicit and every time that the *O. sauteri* individual leaves a patch it reaches a new patch with a prey density (number per leaf) drawn from a clumped (*i.e.*, negative binomial) distribution (for details see below). The number of patches is not predetermined in the simulations and by decreasing the travel times between patches one can take the fact into account that eggplants grow more leaves after planting. All estimated parameter values were from data obtained under approximately 25 °C ambient temperature.
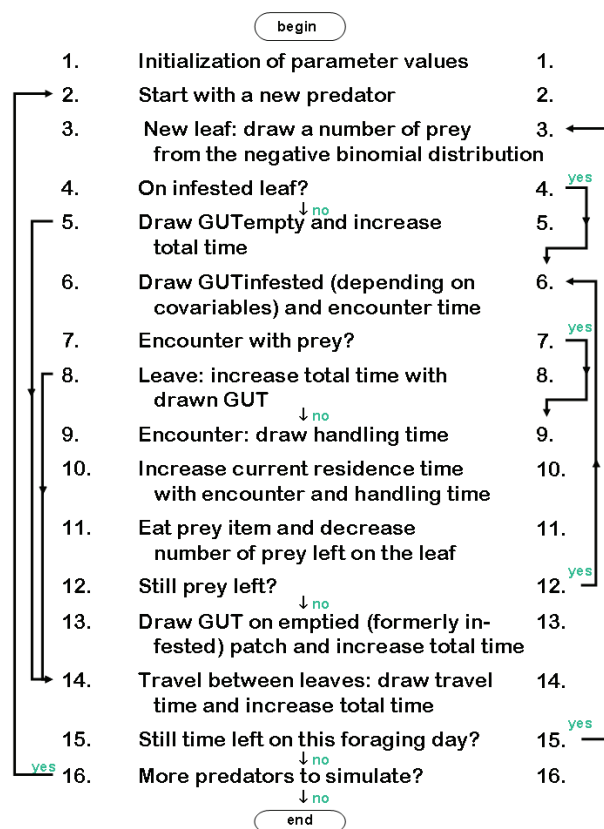

Figure 1. The decision process of the predatory bug *Orius sauteri* is visualised in steps. From simulation of this decision process, a functional response during 1 day of foraging on eggplant leaves in a greenhouse results.

During the simulated day the predator visits prey patches. The number of prey in a patch has a negative binomial distribution according to the mean crowding found by Kawai (1986, see below for details) and patches are encountered in a random way after the predator has travelled during a time span T_{travel} (drawn from an exponential distribution). The decision process for the predator, whether it encounters and eats a prey item or whether it leaves before encountering a prey, is modelled by drawing (1) a value of a giving up time (GUT), and (2) a value of the interval between encounters with prey (IBE). On each leaf the predator encounters and eats a prey item (if drawn GUT is larger than drawn IBE) or leaves the patch (when drawn GUT is lower than or equal to drawn IBE) according to the estimated encounter rate and patch leaving rate from the experiments reported in Yano *et al.* (2005, see also below). The handling time of prey items and travelling time between patches are stochastic and included as part of the simulation.

Parameter values

The parameters that are used in the model are summarized in Table 1, together with their descriptions and estimated values. The rate parameters all describe exponentially distributed durations with a mean that equals the reciprocal of the rate parameter value. *Orius sauteri* is active and forages only during daytime (K Nagai, pers. obs.). Total average time in one foraging day of *O. sauteri* in central Japan in spring to autumn is 14 h (= mean day length) and this is the total time that the predator forages in our simulation.

Patch leaving rate

In Yano *et al.* (2005) a Cox proportional hazards model for patch leaving rate $h(t, pres, time)$ s⁻¹ was fitted to the censored and uncensored giving up times. Here, *pres* is coded 0 or 1, respectively, when prey is absent from or present on the current patch. The variable *time* is the time (in min) since the start of the current leaf visit at the latest renewal point. The parameters β_{pres}, β_{time} and h_0 are the regression coefficients for *pres* and *time* and the baseline patch leaving rate as estimated for the *parametric* survival model [1] that is fitted to the data from the behavioural experiments. The advantage of using a parametric model instead of the semi-parametric Cox's proportional hazards model is that in the parametric model the baseline hazard is also estimated as a parameter from an exponential or Weibull distribution. By having assumed the baseline leaving rate h_0 to be constant, which was warranted by the fact that the scale parameter in a Weibull model was not significantly different from 1, we thus could directly obtain the estimate for h_0. The considered renewal points of the patch leaving process were (like in Yano *et al.* 2005) the entry of a patch and resuming to search after a successful encounter with a prey.

$$h(t, pres, time) = h_0 . \exp(\beta_{pres} . pres + \beta_{time} . time) \qquad [1]$$

Table 1. Description of the parameters in the model.

Parameter [(mean) value]	Description (dimension)
β_{pres} (−1.30)	Regression coefficient of proportional hazards model giving the effect on the baseline hazard rate when prey are present (dimensionless)
β_{time} (0.012)	Regression coefficient of proportional hazards model giving the effect on the baseline hazard rate per minute since patch entry at the latest encounter with prey (min^{-1})
h_0 (1/875)	Baseline hazard rate on empty patch (s^{-1})
r_{enc} (1/709)	Encounter rate with prey items (s^{-1})
r_h (1/200)	Handling rate of prey items (s^{-1})
r_{travel} (1/100)	Travelling rate between patches (s^{-1})
m (number of values[a])	Mean of the negative binomial distribution of thrips over eggplant leaves (number per leaf)
k (number of values[a])	Aggregation parameter of the negative binomial distribution of thrips over eggplant leaves (dimensionless)
T (50400)	Total foraging time in 1 day is 14 h (s)

[a]For relationships between m and k see the main text

The parameter estimates for the β's (β_{pres} = −1.30, β_{time} = 0.012, h_o = 0.001143) are only slightly different from the ones reported as the estimates in Cox's proportional hazards model (Yano *et al.* 2005). To be able to scale up from eggplant leaf level to the greenhouse level the distribution of the GUTs on empty patches is expressed by the estimated baseline hazard h_o, implying a mean GUT of $1/h_o$. The value for the regression parameter β_{pres} indicates that the average giving up time on patches with prey is 3.7 [= $1/\exp(−1.30)$] times larger than on empty patches. Both these average times are influenced by the time (in min) since patch entry: each minute reduces the average time by a factor 0.988 [=$1/\exp(0.012)$].

Other rate parameters

As stated above, both the handling time and the travel time are stochastic and are assumed to follow an exponential distribution. The average handling time of prey is 200 s (Yano *et al.* 2005) and the travelling time between patches is set at 100 s based on the data of walking speed (= 0.2967 cm/s), walking activity (= 0.6933) and mean distance between adjacent leaves (= 20 cm) (K Ohno & E Yano, unpubl.). It was assumed that *O. sauteri* individuals travel by walking between patches based on observation of patch leaving behaviour (E Yano, pers. obs.). For the encounter rate of prey items the same approach is used as in the appendix of Vos & Hemerik (2003). These authors assume that both the intervals between encounters (IBEs) and the giving up times (GUTs) result from an exponential distribution with parameters r_{enc} and h_o, respectively. From our dataset on *O. sauteri* foraging on *T. palmi*, the overall mean $g = 1/(r_{enc} + h_o)$ for IBEs and GUTS together on prey-infested patches was calculated as 539 s and the number of real-

ized IBE-intervals and GUT-intervals in our data is 162 and 52, respectively (fractions 0.76 and 0.24). Under the assumption that both IBE and GUT follow an exponential distribution, we know that the fraction of realized encounters with prey (f_{enc}) and the fraction of realized GUTs ($1 - f_{enc}$) is derived as $f_{enc} = r_{enc} /(r_{enc} + h_o)$ and $1 - f_{enc} = h_o /(r_{enc} + h_o)$, respectively (as proven by Vos & Hemerik 2003; appendix). Therefore, the mean duration of IBE and GUT in all experiments is 709 s ($= g/f_{enc}$) and 2246 s ($= g/(1 - f_{enc})$), respectively. In the simulation we only use the mean value for the IBEs explicitly ($r_{enc} = (1/709)$ s^{-1}; see Table 1), because the other estimate is already simulated with the leaving rate and the effects (β_{pres} and β_{time}) as estimated with the parameterized survival model given in eqn. [1].

Parameterizing the clumped distribution of thrips over leaves

Many insect species have a negative binomial distribution over patches (Harcourt 1961, Atkinson & Shorrocks 1984). For *T. palmi*, Kawai (1986) has investigated their clumped distribution and the author reports about the mean crowding. Here, the formula for finding a patch with *i* prey items when these follow a negative binomial distribution is given for convenience (eqn. [2]). The mean of a negative binomial distribution is *m* prey items, *k* is the clumping parameter, and the variance of the prey items is $\sigma^2 = m + m^2/k$ (Southwood & Henderson, 2000). Note, that when $k \rightarrow \infty$ the negative binomial distribution approaches the Poisson distribution (mean equals variance).

$$P(X=i)=\binom{k+i-1}{i}\left(\frac{k}{m+k}\right)^k\left(\frac{m}{m+k}\right)^i \tag{2}$$

For *T. palmi* Kawai (1986) estimated the functional relationship between the mean crowding m^* and the mean *m* (number of thrips larvae per leaf). He did not compute the clumping parameter of the negative binomial distribution explicitly. Therefore, we have to look into the details of his estimated relationship: the mean crowding m^* is defined as the mean number of neighbouring individuals per individual per quadrat. Its relation to a mean *m* and variance σ^2 is known to be $m^* = m - 1 + (\sigma^2/m)$ (Iwao & Kuno 1968). In general, the relation between the mean and the mean crowding can be described with a simple linear regression: $m^* = \alpha + \beta m$ (Iwao 1977). Thus, if α and β are known, then combination of these two latter equations and the expression for σ^2 yield a relationship between *m* and *k*. For larvae of the species *T. palmi*, Kawai (1986) reported two different estimates for α and β in such a linear regression equation namely $(\alpha, \beta) = (4.11, 1.34)$ or $(4.84, 3.54)$, respectively. The former estimates were obtained from the survey in a greenhouse where the eggplants were just plant-

ed, the latter from the survey in a greenhouse of the later cropping period of eggplants. Combining regression values with the two formulas for mean crowding, the mean and variance of the negative binomial distribution results in two different relationships between k and m, namely $k = m/(4.11 + 0.34m)$ and $k = m/(4.84 + 2.54m)$, respectively. For our simulation study we used these two functions to describe the relationship between mean m and clumping parameter k.

Test of the model

Ideally, the model could be compared with data of one predator that could explore a semi-field set-up with say eight eggplant plants during 6 h. Such data are not available, thus we have only tested the prey consumption and the patch leaving part of our model. Additional data were collected on the number of prey eaten and the patch residence time for patches with 20 prey items as initial density (Jiang & Yano, unpubl.), in a set-up as described in Yano *et al.* (2005). There were 24 replicates. It should be noted that this data set (used for testing the model) has been obtained independently from the data used by Yano *et al.* (2005). To test our model we simulated the numbers eaten and the patch residence times on 1000 patches with initial prey density set to 20. We compared the data and the simulation results for the number of prey eaten with a two sample t-test. For the patch residence times a Kaplan-Meier survivor plot was drawn and the samples were compared with a log-rank test (Klein & Moeschberger 1997). In addition, for the number of prey eaten we have performed 1000 simulations of 25 patch visits on patches with initial density of 20 prey items and compared these 1000 simulation samples with the observed numbers of prey eaten.

Simulation scenarios

We have performed simulations of the searching behaviour of *O. sauteri* at densities below or around the economic injury level of 0.55 2nd instar larvae of *T. palmi* per eggplant leaf for estimating the number of prey eaten by this predator during one foraging day. We also included a mean density of 1/leaf, which is a bit above the normal levels encountered in a greenhouse, to acquire knowledge on how much one adult *Orius* predator is able to eat at a relatively high density. A number of 1000 individual predators were simulated for each combination of m and k. These essentially had access to an unlimited number of leaves with and without prey. For each encountered leaf the number of prey was drawn from a negative binomial distribution.

Sensitivity analysis

Although we are quite sure that the parameter values that describe the searching and decision process of the predator are correct, we have performed a sensitivity analysis on each of the six following parameters h_o, r_{enc}, r_h, r_{travel}, β_{pres} and β_{time}. To get a good view of whether parameter changes cause big variations we varied the parameter values by −50% and +50% at mean densities of prey of $m = 0.1$,

0.5, or 1 prey/leaf with their corresponding *k*-values of the more clumped distributions described by the relation $k = m/(4.84 + 2.54m)$.

RESULTS

Test of the model

We compared the numbers of prey eaten in 25 patch visits on patches with 20 prey items as initial density (n = 1000, overall mean number = 2.97) with the observed numbers of prey eaten (n = 24, mean = 3.46): the median *P*-value in these comparisons was 0.65 (with inter-quartile distance 0.46-0.84). The observed numbers of prey eaten were not significantly different from the simulated data (two sample *t*-test, P = 0.603). For the patch residence times the log-rank test (testing the null hypothesis of no difference between observations and simulations) showed no indication of a significant difference (P = 0.481). The average patch residence time in the simulation was 2742 s and in the observations 2727 s.

Simulation

It should be noted that the different relations between mean *m* and clumping parameter *k* represent more clumped distributions when the *k* value is smaller at the same mean value *m*. Therefore, the second relationship between *k* and *m* represents the more clumped distribution. The number of prey that one predator can eat in 1 day at densities around the economic injury level (m = 0.45-0.65 per leaf) is on average 10 prey per day (range 1-32 prey consumed per day) for both *k* series. The more clumped distribution results in a somewhat lower mean number of prey eaten per day (Fig. 2A) at high mean prey densities, but at low prey densities the results do not differ. The consumed fraction of the total prey pop-
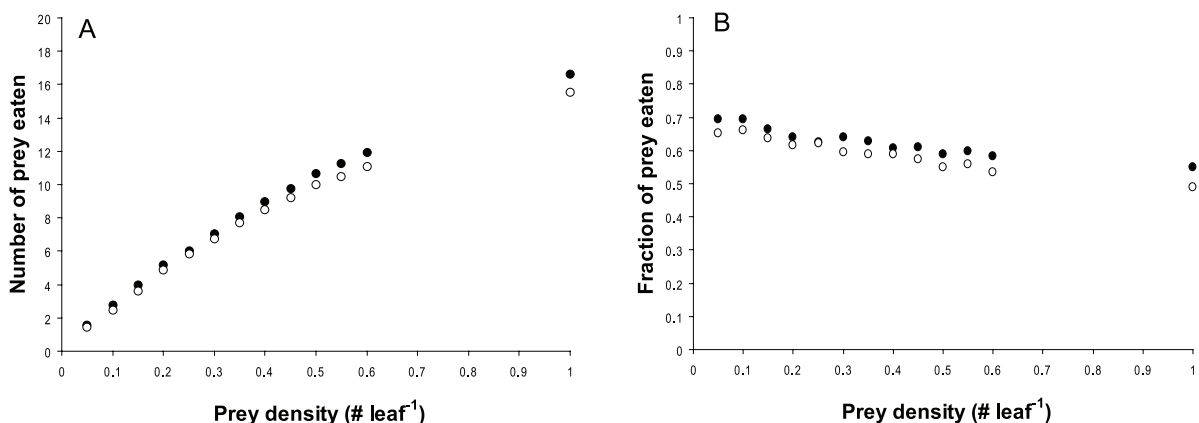

Figure 2. Results of the simulations with a negative binomial distribution of prey over patches with mean density *m* number per leaf on the x-axis and clumping parameter *k* are denoted with filled circles for relationship $k = m/(4.11 + 0.34m)$ and open circles for relationship $k = m/(4.84 + 2.54m)$. (A) Number of prey consumed on average by 1000 simulated *Orius sauteri* in 1 foraging day. (B) Average fraction of the host on the visited patches that is consumed per day by one female *O. sauteri* bug.

Table 2. Results of the sensitivity analysis for the number of prey eaten in one foraging day. The percentage change in each parameter is given for three parameters that we varied.

	h_0		r_{enc}		β_{pres}	
	−50%	+50%	−50%	+50%	−50%	+50%
m = 0.1	−30%	+24%	−31%	+23%	−19%	+25%
m = 0.5	−32%	+15%	−30%	+16%	−18%	+3%
m = 1	−28%	+13%	−32%	+19%	−11%	−3%

ulation that was present on all patches together during the full foraging day was decreasing with the mean prey density m per leaf (Fig. 2B). For both k series the fraction eaten on all encountered leaves together at mean densities around the economic injury level was approximately 55-60%.

Actually, if we assume a homogeneous prey distribution where each patch in the simulation contains the same number of prey items, the functional response becomes a type-I response, and the predator can reach unrealistically high levels of around 80 prey items eaten per day if gut content is not limiting (data not shown).

Sensitivity analysis

For the most clumped k series we have changed the values of the six parameters h_o, r_{enc}, r_h, r_{travel}, β_{pres} and β_{time} by −50 or +50%. Varying the parameter β_{time}, that increases the leaving tendency during the course of a patch visit, only caused a change in the number of prey eaten in the range of −3 to +3% at the five investigated mean prey densities. Handling time modelled as the rate r_h affects the fraction of prey eaten by differences in ranges from −10 to +1%. The number of prey eaten when changing the travel times as given by the rate r_{travel} varied between −9 and +7%. Thus these parameters did not have a great effect on the number of prey eaten. Table 2 shows the results of how changes in the baseline leaving tendency h_o, the prey encounter rate r_{enc} and the behavioural parameter that makes an individual search longer in a prey-infested patch β_{pres} affect the mean number of prey eaten by one individual *O. sauteri* predator. All three of these parameters influence the resulting number of prey eaten to a greater extent (ranges h_o: −30 to +24%, r_{enc}: −34 to +23%, and β_{pres}: −19 to +25%) than the formerly reported parameters. As expected, increasing (decreasing) the baseline hazard rate on empty patches h_o or the encounter rate r_{enc} directly results in an increase (decrease) of the number of prey eaten. An increase in the regression parameter for the presence of prey in a patch β_{pres} cannot be interpreted in a straightforward manner, because an increase in the negative value by 50% means that initially the giving up time on patches with prey is multiplied by seven (= 1/exp(−1.3*1.5), eqn. [1]). For low mean prey densities this results in higher numbers eaten per day but for high mean prey densities more time is wasted after some time on an eggplant leaf. In Fig. 3 it is shown how the result-

Table 3. Results of the sensitivity analysis for the fraction eaten of the total number of prey that is encountered in one foraging day. The percentage change in each parameter is given for three parameters that we varied.

	h_0		r_{enc}		β_{pres}	
	−50%	+50%	−50%	+50%	−50%	+50%
$m = 0.1$	+19%	−13%	−24%	+12%	−25%	+18%
$m = 0.5$	+35%	−17%	−29%	+17%	−27%	+28%
$m = 1$	+36%	−17%	−30%	+20%	−28%	+30%

ing number of prey eaten per day by one O. *sauteri* depends on the value of h_o and β_{pres} in our simulations.

How the parameter values influence the fraction eaten by one individual O. *sauteri* predator on the total number of prey encountered in the visited patches is shown in Table 3, for the three most influencing parameters: the baseline leaving tendency h_o, the prey encounter rate r_{enc} and the behavioural parameter that makes an individual search longer in a prey-infested patch β_{pres} (ranging from −17 to +36%, −30 to +20%, and −28 to +30%, respectively). Varying the parameter β_{time} only caused a change in the range of −5 to +8% at the investigated mean prey densities. The handling time modelled as the rate r_h and the travel times as given by the rate r_{travel} affect the fraction of prey eaten only slightly (ranging from −4 to +4%). As an illustration, the fraction prey eaten from what is encountered increases with a bigger negative number for β_{pres}, because the predator is more persistent in searching for prey on encountered leaves.
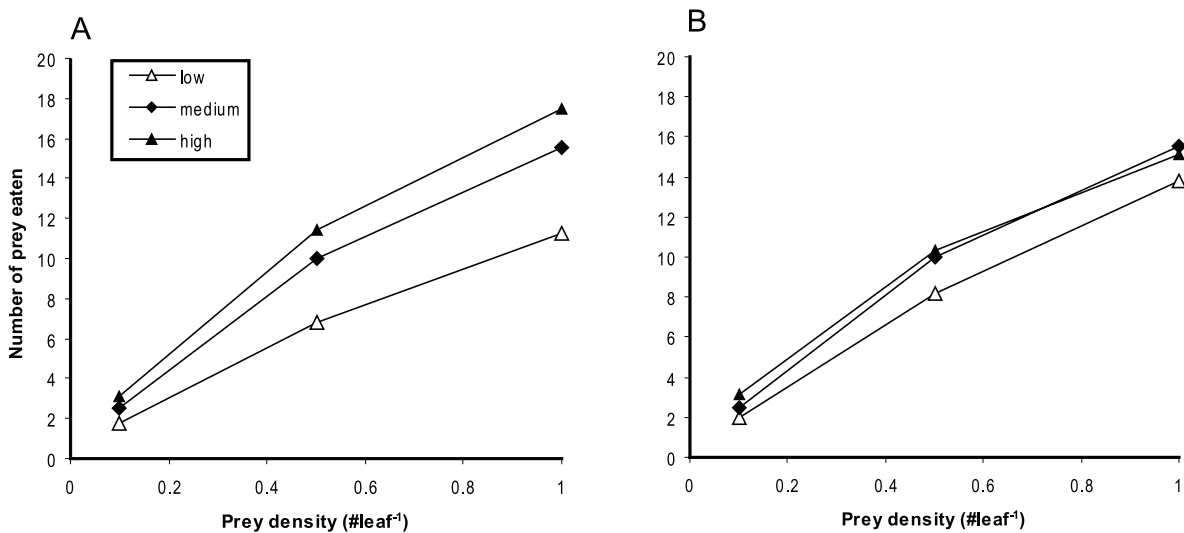

Figure 3. Examples of results of the sensitivity analysis for the series with the mean density *m* and the *k* values from the more clumped distribution: (A) the influence of the baseline leaving tendency h_o, and (B) the influence of the presence of prey β_{pres} on the number of prey eaten (low, medium and high stand for 0.5, 1 and 1.5 times the default value, respectively).

DISCUSSION

The simulation results of the model depicted in Fig. 1 show that one female adult of *O. sauteri* can find and eat approximately 10 prey individuals per day at the level of infestation around the economic injury level of *T. palmi* (an average of 0.55 individuals per leaf). Since the intrinsic rate of natural increase of *T. palmi* at 25 °C is estimated at 0.102 per day (Kawai 1986), it is calculated that the *T. palmi* population increases only by approximately 0.11 per day. Within the proper ratio of the number of *O. sauteri* to *T. palmi*, *O. sauteri* has great potential for suppressing the *T. palmi* population. We have not included interference and competition between predators. When predators compete with each other this might reduce the number of prey eaten per day per individual. However, densities of the predator in biological control are generally not so high. For example, in the study by Kawai (1995), the maximum density of the total of nymphs and adults of *O. sauteri* per eggplant leaf in five greenhouses was 0.21 when 0.5 or 1.0 nymphs per leaf were released once in each greenhouse.

Because the experimental arena in most of the functional response studies in the laboratory were very small, homogenous spaces such as a Petri dish or a plastic vial to which the *Orius* individual was confined (McCaffrey & Horsburgh 1986, Isenhour *et al.* 1989, 1990, Coll & Ridgway 1995, Nagai & Yano 2000, Gitonga *et al.* 2002), experienced prey densities were higher than actual densities in greenhouses or in fields around the economic injury level. In the experiments of Nagai & Yano (2000), the possible lowest density of thrips was three individuals per leaf, which is approximately 5× the economic injury level. In addition, *Orius* individuals could not leave a patch (or arena) and were forced to search on the existing patch. Another difficulty in these laboratory experiments is that the total number of available prey items is limited. The predator often consumes all prey items in one patch when prey densities are low. In the greenhouse and in the field, however, the number of prey is almost unlimited even at a low average prey density. Therefore, it is impossible to evaluate the predation capability of *Orius* spp. at low prey density in the described laboratory experiments. This simulation study assumes that a female adult of *O. sauteri* moves from one patch to another in an environment comprising of an unlimited number of patches with different prey densities that are drawn from a negative binomial distribution. The distribution of thrips on patches based on Iwao's patchiness regression (Kawai 1986) allowed us to simulate a realistic foraging environment for *O. sauteri*. In this way we were able to evaluate the predation capability of *O. sauteri* at low average *T. palmi* densities per eggplant leaf, *i.e.*, around its economic injury level. It has been shown that *O. sauteri* has a great capability of predation at such low prey densities.

Most experimental studies have shown a type-II functional response by *Orius* spp. to densities of different types of prey (McCaffrey & Horsburgh 1986, Isenhour *et al.* 1989, 1990, Coll & Ridgway 1995, Nagai & Yano 2000, Gitonga *et*

al., 2002). Among them, Nagai & Yano (2000) have studied the functional response of *O. sauteri* to densities of *T. palmi* and found a type-II response for a female adult foraging at densities of the 2nd instar larvae at 25 °C. The current simulation study also results in a type-II response of *O. sauteri* foraging at low densities of *T. palmi* around its economic injury level. It was also shown that the distribution of *T. palmi* among patches has a great influence on the shape of the functional response.

In the modelling studies of the foraging behaviour of *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) attacking immatures of the greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood) (Homoptera: Aleyrodidae), functional responses of *E. formosa* to whitefly immature densities were affected greatly by host distribution over leaflets as those of *O. sauteri* to densities of thrips larvae (van Roermund *et al.* 1994, 1997).

The results of the tests for the model strengthens our opinion that the details of the simulation model are resembling the behaviour of *O. sauteri* foraging on eggplant leaves under an ambient temperature of 25 °C. In addition to this fact it is no surprise that the model outcomes are highly sensitive to the values of the baseline patch leaving rate h_0 and the encounter rate r_{enc}. When the encounter rate is higher at the same baseline patch leaving rate then more prey can be encountered and both the number of prey eaten and the fraction of the total prey population on the visited patches increases. If alternatively the baseline patch leaving rate is higher at the same value of the encounter rate, then a patch is left earlier. Thus, the number of patches that are visited in the same amount of time and the total number of prey eaten both increase, but the consumed fraction of the total prey population on the visited patches decreases. How the number of prey eaten is influenced by the value of β_{pres} is not so clear: the encounter rate with prey is only defined on prey-infested patches and this behavioural parameter influences the leaving tendency on such patches. Therefore, the resulting effect on the number of prey eaten in 1 day after having visited prey-infested and empty patches is not straightforward. The consumed fraction of prey is higher when β_{pres} is higher because the predator prolongs its giving up time on prey-infested patches (note that the value of β_{pres} is negative to begin with).

In the study of van Roermund *et al.* (1997) at high host densities with a clustered distribution of hosts over leaflets, the giving up time (GUT) on a leaflet was the most essential parameter influencing the parasitoid-host dynamics. Outcomes of our study are also highly sensitive to the value of the baseline patch leaving rate h_0 (the rate of leaving empty patches). Other parameters could not be compared with the results of van Roermund *et al.* (1997) because of differences in model structures and in foraging behaviour of *E. formosa* and *O. sauteri*, respectively.

With this simulation study we have quantified the daily value of the functional response for a general predatory anthocorid bug, suggesting that this value

allows for effective control of thrips by such a predator. The previously performed behavioural analysis (Yano *et al.* 2005) served as a starting point for the quantification of the impact that one individual *O. sauteri* has on its prey population at an ambient temperature of 25 °C.

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