Biocontrol of western flower thrips by heteropteran bugs
van den Meiracker, R.A.F.

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Do functional responses of predatory arthropods reach a plateau? A case study of Orius insidiosus with western flower thrips as prey

Parameters determining the functional and numerical response of Orius insidiosus to the density of second instar larvae of the western flower thrips (WFT), Frankliniella occidentalis, were estimated with the aim to be used in models calculating adequate release ratios of predators vs prey. Especially when the prey population must decrease immediately after predator release and the time to suppression must be short, it is of crucial importance to know whether the functional response reaches a plateau or keeps on increasing with prey density within the range of densities that are realistic for the prey. Such plateaus may arise from constraints on the time budget or from constraints on gut-fullness-associated motivation to attack the prey. Estimates of the plateau for O. insidiosus based on prey handling times by far exceed realistic values. In addition, motivation constraints did not apply, because the level of gut fullness above which attack ceases coincides with gut capacity. This implies that the predation rate keeps on increasing linearly with the square root of the density of WFT-larvae and does not reach a plateau within the realistic range of thrips densities (0-20 WFT per cm²). Such plateaus are likely to occur for smaller-sized predators and smaller-sized stages of the same predator and they may also occur when the prey stage offered has better capacities to escape or resist attack. We argue that the presence and level of plateaus in functional responses are of importance for determining initial predator-to-prey ratios.

Orius insidiosus (Say) (Heteroptera: Anthocoridae) and various other Orius spp. are effective biological control agents of western flower thrips (WFT), Frankliniella occidentalis (Pergande) (Thysanoptera: Thripidae) on sweet pepper crops in greenhouses (Van den Meiracker & Ramakers, 1991; Riudavets, 1995). To quantify the impact of these anthocorid predators it is important to assess their functional and numerical response to thrips density. These responses describe how the number of prey captured and the number of predator offspring change with prey density. These responses describe how the number of prey captured and the number of predator offspring change with prey density (Solomon, 1949). Holling (1959a,b, 1966) described three types of functional responses, of which type II (predation rate increasing to a maximum at a decreasing rate) has long been considered as typical for insect predators. However, type III responses (sigmoid) also occur (Hassell et al., 1977). All these responses are characterized by the presence of a plateau at high prey densities, which may either originate due to time constraints or to food processing constraints (Holling, 1959a,b, 1966).

When the predator is limited by the available time, then the plateau is determined by the ratio of the total time and the time spent handling a prey. For a constant search rate the functional response exhibits a negatively accelerated increase.
to this plateau (type II; Holling, 1959b). However, in many predatory arthropods handling time comprises only a small proportion of the total time available. Handling times in Orius are also relatively short. Isenhour & Yeargan (1981a) found average feeding times of hungry females of *O. insidiosus* on adult thrips ranging from 9 to 19 min, whereas capture took only a few seconds and pursuing rarely occurred. This would imply a maximum predation rate of 76-160 thrips per day. Orius predatory bugs often consume their prey only partially, and sometimes they do not even feed on prey killed (Simpson & Burkhardt, 1960; Rajasekhar & Chatterji, 1970; Askari & Stern, 1972; Manley, 1976; Isenhour & Yeargan, 1981b; Knutson & Gilstrap, 1989), which will reduce handling time considerably. When prey density increases, the proportion of thrips that is completely consumed by *Orius minutus* (L.) decreases (Lichtenauer & Sell, 1993), and feeding time will decrease as well. Thus, since handling time decreases with gut fullness, the upper level due to time constraints increases with prey density. So, even at high prey densities total handling time will comprise only a small proportion of the time budget. Alternatively, it is the search rate that decreases with gut fullness, which constrains the functional response (Sabelis, 1992).

Mechanistic models of how the predator's level of gut fullness (satiation) influences the rate of prey capture have proven quite successful in predicting the shape of functional responses of predatory mites and praying mantids to the density of their prey (Metz & Van Batenburg, 1985; Sabelis, 1986, 1992). For the special case where the time spent handling prey is negligible and the food deficit of the gut does not exceed the food content of the prey, there exists an analytic solution of the functional response model. This solution only requires estimates of gut capacity, rate of gut emptying, and the relation between satiation and the prey capture rate (Metz et al., 1988; Sabelis, 1992). In this paper we estimate these parameters, as well as the efficiency of converting ingested food into egg biomass, in an attempt to assess whether predation is constrained by food processing or time budget.

The importance of these constraints critically depend on the prey density range, as manifested under realistic conditions. Rosenheim et al. (1990) found WFT densities on cucumber leaves up to c. 0.25 per cm² whereas in flowers on average 50-fold higher densities were reached. According to Van den Meiracker & Ramakers (1991) mean densities on sweet pepper leaves are much lower than in flowers where they can be as high as 42 thrips per flower (mobile stages). Individual flowers may harbour as much as 120 thrips, which would represent a density of c. 20 per cm² flower surface (Van den Meiracker, pers. obs.). In this paper, we will investigate whether or not the predation rate reaches a plateau in the range of thrips densities from 0 to 20 thrips per cm².

**MATERIALS AND METHODS**

Predatory bugs were obtained from a stock colony, initiated in 1989 with *O. insidiosus* from R.D. Oetting (Georgia, USA). For rearing details see Van den Meiracker & Ramakers (1991). WFT was obtained from C. Mollema (Wageningen, The Netherlands) and reared on cucumber (*Cucumis sativus* L.) fruit sections of approximately 5 cm in length, whereas bee-collected pollen was provided as
additional food. Second instar WFT larvae were collected for experiments 6-7 days after birth. Their average length was 1.05 mm, which corresponds with 23 μg according to P.C.J. van Rijn (unpubl.). Rearing and experimental conditions were 25°C, 75% r.h., and L16:D8.

**Gut content and relative rate of gut emptying**

*Orius insidiosus* females were collected from the stock colony approximately one week after adult eclosion. During 24 h they were satiated in 25 ml glass vials with a leaf disc (24 mm diam., *Phaseolus vulgaris* L.) on a layer of c. 5 ml agar with an excess of second instar WFT larvae. Then, they were starved in empty vials for a period of 6, 12, 24, or 48 h, and, finally, their weight was determined. They were satiated again by 1 h feeding on WFT larvae, and weighed to determine the amount of food ingested. Each starvation series was started with 16 females, but females that did not oviposit during the first saturation period were discarded. In preliminary experiments with *Ephestia kuehniella* Zeiler eggs it was found that not all females had increased in weight after the second satiation period. Therefore, to ensure satiation, females with a weight increase less than half the maximum in their series were discarded.

The data were fitted to the equation

\[ h(t) = m(1 - \exp(-dt)) \]

(Holling, 1966) using iterative least-squares regression, where \( h \) is the amount of food consumed after a starvation period \( t \), \( m \) is gut capacity, \( d \) is the rate constant of gut emptying. This provides estimates of \( m \) and \( d \). The amount of food in the gut (or satiation \( s \)) can be described as

\[ s(t) = m \exp(-dt) \]

**Rate constant of prey capture**

Experiments were carried out on floating leaf discs (*P. vulgaris*, area 10 cm²) with 20 second instar WFT larvae. Adult females of *O. insidiosus* (one week after adult emergence) from the stock colony were fed with an ample supply of WFT larvae, as described above. After 24 h, fresh WFT larvae were provided during 4 h to ensure full satiation. Females that did not oviposit were discarded. The satiated females were starved in empty 25 ml glass vials 0-5 h before they were allowed to search on the floating leaf disc. Each female was observed for 30 min, or until first prey capture. Encounters with prey (successful or unsuccessful) were recorded in deprivation time classes of 30 min. Care was taken to obtain a more or less equal number of encounters per deprivation time class. These time classes were transformed to classes of satiation level using Equation (2). For each class the rate constant of prey capture \( g(s) \) was calculated as the number of captures divided by the observation time multiplied by the prey density in the experiment (2 cm²). The capture success ratio (CSR) as a function of the deprivation time was also determined. The CSR is the fraction of encounters with prey that results in killing of the prey.
Parameter estimation of the functional response

A simple approximation of the functional response follows from the following two assumptions: (1) time spent in attack and handling of a prey item is negligible, and (2) the gut should be filled with an amount of food not more below gut capacity than the content of a single prey. A justification of these assumptions is given in the Results section. An estimate of the predation rate \( F \) can be made using the approximations given in Metz et al. (1988):

\[
F(D) = \frac{d}{\ln\left(\frac{m}{c}\right) + \sqrt{\frac{\pi d}{2bcD}}}
\]

Here \( D \) is the prey density, \( c \) is the capture threshold (the level of gut fullness above which the rate constant of prey capture \( g(s) \) is zero), \( b = -g'(c) \), and \( g'(c) \) is the differential of \( g(s) \) at \( c \). If the capture threshold coincides with the gut capacity \( (c = m) \), Equation (1) reduces to:

\[
F(D) = \sqrt{\frac{2d bc D}{\pi}}
\]

In this case the predation rate is linearly related to the square root of prey density. Note that the square root function is not unique for predation models that take gut fullness into account. Alternative assumptions – not relevant to the biological system under study – can lead to the derivation of a similar functional form (Lundberg & Åström, 1990).

Assessment of food conversion efficiency

The testing arenas consisted of 25 ml glass vials, closed with snap caps. Ventilation was provided via a hole in the cap covered with fine nylon gauze. The vials were filled with 12 ml agar as a substrate for a leaf disc (24 mm diam., \( P. vulgaris \)). Second instar WFT larvae were put on the leaf discs at densities of 0, 3, 6, 12, and 24 per vial.

\( Orius insidiosus \) females were kept with a male and excess of \( E. kuehniella \) eggs during the first four days after adult eclosion, whereas pieces of bean pod (\( P. vulgaris \)) were provided for oviposition. Only females that oviposited within these four days were used in the experiments. Subsequently, on the first day of the experiment, the females were transferred to the testing arenas. Twelve females were used as replicates at each prey density. On the second and third day of the experiment the females were transferred to fresh testing arenas. The number of WFT larvae killed and the number of \( Orius \) eggs inserted into the leaf discs were counted each day. All series were run simultaneously. Preliminary experiments revealed that WFT mortality per day in absence of predatory bugs was negligible.

The density of WFT larvae was calculated, assuming that both WFT larvae and predatory bugs did not leave the leaf disc. The mean time interval between prey captures was estimated as the reciprocal of \( F(D) \), whereas \( D \) was recalculated after each prey capture. The decrease of the amount of food in the gut during that interval was calculated using Equation (2). It was assumed that after each prey capture the gut was filled with 23 \( \mu g \) (weight of a second instar WFT) or to its capacity. This
enabled calculation of the mean daily level of gut fullness during the 3 days of the experiment at each density. The data of the last 2 days were used to assess the relation between food digestion and egg production, and hence the food conversion efficiency.

RESULTS

Gut content and relative rate of gut emptying

The amount of food required to fill the gut after a period of starvation is shown in Fig. 1. Equation (1) with $m = 62.3 \, \mu g$ and $d = 0.0580 \, h^{-1}$ gave a fit with $R^2 = 0.743$ ($n = 45$).

Figure 1. Amount of food from second instar WFT larvae required to fill the gut of Orius insidiosus to its capacity (means ± s.d.) after a period of starvation. Regression curve: $y = 62.3(1-\exp(-0.0580x))$, $R^2 = 0.743$, $n = 45$. 

rate constant of prey capture

During 1892 min, 154 females had 1076 encounters with WFT larvae, of which 111 resulted in capture of the prey. The rate constant of prey capture decreased linearly with satiation in the observed interval, and did not become zero until the gut was completely filled (Fig. 2). A linear regression line was fitted by forcing through the satiation axis at $s = m$. The CSR increased with deprivation time (Fig. 3). It was observed a few times that a predatory bug pierced a WFT larvae and almost immediately withdrew its stylet, suggesting that food uptake was little or none.

Parameter estimation of the functional response

The approximations given by Metz et al. (1988) are based on the reasonable assumption of negligible handling times and the special assumption of a food deficit of the gut that does not exceed the food content of the prey. Since the food content of the second-instar larva (1.05 mm length) equals 23 µg, a satiated predator would exceed this threshold only after c. 8 h starvation. In other words, the model applies to a predator feeding on a minimum of c. 3 thrips larvae per day.

Figure 2. Rate constant of prey capture as function of gut content in adult female Orius insidiosus with second instar WFT larvae as prey. Linear regression line: $y = 14.2 - 0.228x$, $R^2 = 0.872, n = 11$. 
Because the capture threshold equals the gut capacity (Fig. 3) Equation (4) was used to calculate the functional response. The estimate of \( g'(c) \) was -0.228. Under steady state conditions the functional response to second instar WFT larvae can be described as \( F(D) = 0.724 \sqrt{D} \text{ h}^{-1} \) or \( 17.4 \sqrt{D} \text{ day}^{-1} \) (Fig. 4).

**Assessment of food conversion efficiency**

The predation experiments showed that all WFT larvae were killed at thrips densities of 3, 6, and 12 during each of the three consecutive days whereas only at the density of 24 per vial some larvae escaped attack (averages of 22.4, 22.2 and 23.0 WFT larvae on the first, second and third day respectively). It also showed that egg production in absence of prey was much higher on the first day of the experiment (6.9 eggs) than on the next two days, where 2.7 and 1.8 eggs were laid respectively. This suggests that egg production on the first day is influenced by food (E. kuehniella eggs) acquired before the experiment. As this does not relate to the experimentally imposed food regimes, we discarded the data of the first day from further analysis.

![Figure 3. Capture success ratio of adult female Orius insidiosus feeding on second instar WFT larvae as function of deprivation time. Linear regression line: \( y = 0.0598x, R^2 = 0.737, n = 11 \).](image-url)
Based on the formula for the functional response (and its underlying assumptions!) tentative estimates were made of the time intervals between successive prey captures. According to this assessment, all WFT larvae would be killed at densities of 3, 6, and 12, whereas 23 larvae would be killed at the highest density, which agreed with the experimental data. The decrease of the food content of the gut during the intervals between prey captures, as well as the amount of thrips content that entered the gut during feeding events were calculated (assuming that the prey was either emptied completely or partially in case the predator's gut becomes filled to capacity). In this way mean food contents of the gut were calculated for each prey density and for each consecutive day and these were plotted against the number of eggs produced on the same day (Fig. 5). Assuming that the food digested is first allocated so as to compensate for weight loss (defecation, evapo-transpiration) and that the surplus is used for production of eggs of constant size, a linear relation between egg production and food digested is expected. This linear relation should cross the x-axis at a positive value of the mean level of gut fullness. However, when the gut is virtually empty the predators appear to produce still c. 2 eggs. This suggests that either available food reserves are re-utilized or that a series of nearly finished eggs are longer retained and not resorbed. For these reasons we discarded the data points at nearly empty guts and used the remainder for fitting a linear relation. This line shows that there is a minimum level of c. 18 μg food in the gut below which egg production ceases and that above this threshold egg production increases with one unit for every increase of gut fullness equal to 4.8 μg.

![Figure 4](image.jpg)

Figure 4. Functional response of adult female *Orius insidiosus* to the density of second instar WFT larvae, estimated using the approximation of Metz et al. (1988).
DISCUSSION

The most salient conclusion of this experimental analysis of parameters determining the functional response of *O. insidiosus* is that the capture threshold coincides with gut capacity \( (c = m) \). This necessarily leads to the prediction that the functional response will not reach a plateau in the range of realistic densities due to satiation of the predator. Instead it will keep on increasing linearly with the square root of the thrips density. This implies an increase at a decreasing rate, provided the time spent handling does not impose a next constraint. Under these assumptions the predicted rate of predation at a density of 20 thrips larvae per cm\(^2\) is equal to 78 thrips larvae per day. Based on data of Isenhour & Yeargan (1981a) the plateau due to handling time constraints would be at 76-160 thrips per day. The lower bound seems close to the predation rate at 20 thrips per cm\(^2\) predicted for negligible handling times, but one should realize that (1) the handling times were measured for hungry females and satiated females normally take much less time, and (2) the adults thrips used by Isenhour and Yeargan may well be more difficult to subdue and feed upon than the second-instar larvae used by us. Hence, we predict that handling time constraints occur at much higher densities than 20 thrips larvae per cm\(^2\) and that the predation rate does not reach a plateau in the range of realistic densities of thrips larvae (Fig. 5).

![Figure 5. Relation between the estimated mean daily gut content and daily oviposition (means ± s.d.) in Orius insidiosus. Data of the second and the third day of females provided prey were used for linear regression \( (y = -0.377 + 0.208x, R^2 = 0.451, n = 92) \).](image-url)
One would expect that the larger the prey stage, the more difficult it will be to seize it by a given size of the predator, as shown by Dixon & Russel (1972) and Evans (1976) for of Anthocoris nemorum (L.) and Anthocoris confusus Reuter preying on aphids. Hence, it may be hypothesized that the capture threshold will be smaller than gut capacity \((c < m)\) when the prey becomes harder to subdue. Thus, to observe functional responses with a plateau one should consider prey or prey stages with a larger body size relative to the predator. Indeed, Isenhour & Yeargan (1981b) found quite good evidence for a plateau when adult thrips were used, rather than the larvae. It is reasonable to assume that adults have a greater ability to escape because they are winged and move faster. Hence, the adults will be more difficult to seize successfully and the predator may refrain from attack before being fully satiated, because the energy involved in attack exceeds the energy to be gained from feeding. The plateau in the data obtained with females of O. insidiosus by Isenhour & Yeargan (1981b) was \(c. 35\) thrips adults per day, based on our visual inspection of the 4 high density points in their graph, and \(57\) thrips per day according to their fit of a Type II Holling curve. In addition, their predation curves for males of O. insidiosus reaches a lower plateau than the females \((c. 22\) per day according to visual inspection of their graph and \(35\) per day according to their fit of the Type II Holling curve). This is expected because males are somewhat smaller than females and therefore have even more difficulty in seizing adult thrips. Moreover, males have a smaller gut capacity and require less food.

For much the same reasons one would expect that the younger the predator, the smaller it is and the more difficult it will be to attack a prey of given size, as shown by Dixon & Russel (1972) and Evans (1976) for A. nemorum and A. confusus preying on aphids. At some point this will imply that the capture threshold shifts below gut capacity, thereby changing the functional response from a root function to a saturation curve. Also it is expected that saturation curves will be more frequently observed for the case of small-sized predators of thrips. This is indeed the case for phytoseiid mites, where capture thresholds of females of Amblyseius barkeri (Hughes) and Amblyseius cucumeris (Oudemans) are shown to be lower than gut capacity \((Bakker & Sabelis, 1989; Van der Hoeven & Van Rijn, 1990; P.C.J. van Rijn, unpubl.) and the functional response exhibits a clear-cut plateau even for first-instar WFT larvae (P.C.J. van Rijn, unpubl.).

Constraints on the functional response to prey density obviously matter to the ability of the predators to suppress prey populations at a local spatial scale where strong coupling of predator and prey populations is possible. If constraints due to time budgets or satiation are absent, then the predation rates keep on increasing with prey density. This is the case for females of O. insidiosus preying on second-instar WFT larvae within the density range considered to be realistic. However, phytoseiid mites are subject to satiation constraints and reach a plateau at very low thrips densities. These differences will really matter in biological control programs where predators are used to obtain a decrease of the pest population immediately after predator introduction. Especially, when the time to suppression of the pest population must be short, then these predation characteristics are of decisive importance for determining the initial predator-to-prey ratio \((Sabelis & Van Rijn, 1997; P.C.J. van Rijn, R.A.F. van den Meiracker, P.M.J. Ramakers & M.W. Sabelis, unpubl.)\).
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