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Is arthropod predation exclusively satiation-driven?

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Functional response models differ in which factors limit predation (e.g. searching efficiency, prey handling time, digestion) and whether predation behaviour is governed by an internal physiological state (e.g. satiation). There is now much evidence that satiation is a key factor in understanding changes in foraging behaviour, and that many predators are effectively digestion limited. Here, we ask if predation in a predatory arthropod can be explained from satiation-driven behaviour alone, or if behaviour is also influenced by the density of prey other than via the effect of prey ingestion on satiation. To address this question a satiation-based predation model is formulated, for which parameters are estimated on the basis of observations on digestion rate, satiation-related prey searching rate and prey capture behaviour, basically under high prey density conditions. The model predictions are subsequently tested against longer term predation experiments carried out at high and low prey densities. Since satiation can easily be linked with egg production, these tests are carried out both for predation and oviposition.

The predator–prey systems under study consist of females of two predatory mite species (*Neoseiulus barkeri* and *N. cucumeris*) and the larvae of two thrips species (*Thrips tabaci* and *Frankliniella occidentalis*) as their prey. For *N. barkeri* foraging on *T. tabaci*, the model gives good predictions at both high (4 larvae cm^{-1}) and low (0.1–1 larvae cm^{-2}) prey densities. For *N. cucumeris* foraging on *F. occidentalis*, the predictions hold at the high prey density, but are too low at low prey densities. Thus our analysis indicates that we cannot fully explain density-dependent predation rates from satiation-driven behaviour alone. Different mechanisms are suggested on how prey density may affect foraging efficiency other than via satiation.

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Functional response models differ in which factors limit predation and whether predation behaviour is governed by an internal physiological state (e.g. satiation). Traditionally, predators are assumed to be time-limited, as in Holling's (1959) disk equation, where the predation rate is limited by the (effective) searching rate at low prey densities and limited by the time needed to handle prey at high prey densities. Since handling goes at the expense of the time available for searching, predation rate will level off at high prey densities, and the rise to the plateau obeys the law of diminishing returns (type II response), assuming that searching rate and handling time are not affected by prey density (Hassell et al. 1976).

Although Holling's time budget models are simple and describe functional response curves of many predators reasonably well (Hazzard and Ferro 1991, Shipp and Whitfield 1991, Mansour and Heimbach 1993, Fan and Petitt 1994, Nwilene and Nachman 1996a, Opit et al. 1997, Messina and Hanks 1998, Castagnoli and Simoni 1999, Montserrat et al. 2000), they do not capture the essence of the predation process. This is because predators are often not primarily time-limited, but

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digestion limited (Sabelis 1992, Jeschke et al. 2002). For example, requiring 5 minutes to consume a spider mite egg, the predatory mite *Phytoseiulus persimilis,* can potentially kill 20 per hour, whereas in reality it kills (under steady-state conditions) maximally one per hour (Sabelis 1986). Time spent on other events like handling noncaptured prey, cleaning or oviposition cannot explain the discrepancy as they take only seconds or minutes per event. Holling (1966) was among the first to recognise this problem, and considered gut fullness or satiation as an important intermediate state variable. Taking the praying mantid *Hierodula crassa* as a model organism, he studied a great number of behavioural components of predation in relation to satiation, and by incorporating these data into a stochastic simulation model he was able to predict predation rates quite well. Similar results were obtained by Fransz (1974) modelling a system of predatory mites and spider mites. These simulation models of Holling and Fransz were later simplified by use of discrete, stochastic queuing theory (Curry and DeMichele 1977, Sabelis 1981, 1985, 1986, 1990) and by a continuous approximation using physiologically structured models framed in partial differential equations (Metz and Van Batenburg 1985a, b). The latter framework allowed the derivation of simple, limiting-case approximations (Metz et al. 1988), such as the square root function, the shape of which fundamentally differs from the disk equation. The square root model was tested for predatory mites (Metz et al. 1988, Sabelis 1992) and predatory bugs (Van den Meiracker and Sabelis 1999). All these model validations together have provided strong evidence that various components of foraging behaviour are a function of satiation and these satiation-driven functions are essential to understand the predation process.

In this article, we ask if predation can be explained from satiation-driven behaviour alone. In other words, does the prey environment alter foraging behaviour only by altering satiation or also in other (more direct) ways? This question is answered by testing a satiation-based predation model with parameters estimated at high prey density against independent predation experiments carried out at high and low prey density. Since the turnover of prey into eggs is very fast in predatory mites, and the model allows calculation of this turnover, the tests are carried out both for predation and oviposition. The predator–prey systems under study consisted of females of two predatory mite species (*Neoseiulus barkeri* and *N. cucumeris*) and the larvae of two thrips species (*Thrips tabaci* and *Frankliniella occidentalis*) as their prey.

Satiation-driven predation model

Assuming mass action (random search and homogeneous mixing) the predation rate (F) can be written as the product of prey density (x) and rate of effective search (g):

$$F(x) = x \times g(s) \tag{1}$$

where the rate of effective search is a function of the predator's satiation ($s \in [0;1]$), which is zero at or near full satiation. Satiation, in turn, is affected by predation (and thus by prey density) as well as by gut clearing.

To describe the relationship between the rate of effective search and satiation, g(s), we used the following 'prey capture function' (Sabelis 1981, 1990, Dicke et al. 1989, Fig. 1):

$$g(s) = \begin{cases} b\dfrac{c - s}{1 + zs} & s < c \\ 0 & s \geq c \end{cases} \tag{2}$$

At $s = c$, the so-called capture threshold, g(s) becomes zero. The shape of the positive part of the function is determined by z: concave when $z \in \langle -1; 0 \rangle$ and convex when $z \in \langle 0; \infty \rangle$(Fig. 1). Parameter b defines the maximum value of g(s).

The amount of food ingested per captured prey (relative to the maximum gut content) is either limited by the food content of the prey (w_p) or by the gut capacity, in which case

$$w(s) = 1 - s \tag{3}$$

Gut clearing is assumed to be an exponential process with the relative rate of gut clearing a. Thus in the absence of prey ingestion this yields

$$\frac{ds}{dt} = -as \tag{4}$$

Since total prey handling time takes less than 5% of the time available for search (Sabelis 1986, 1992, P. C. J. van Rijn, pers. obs.), and can therefore be ignored, prey

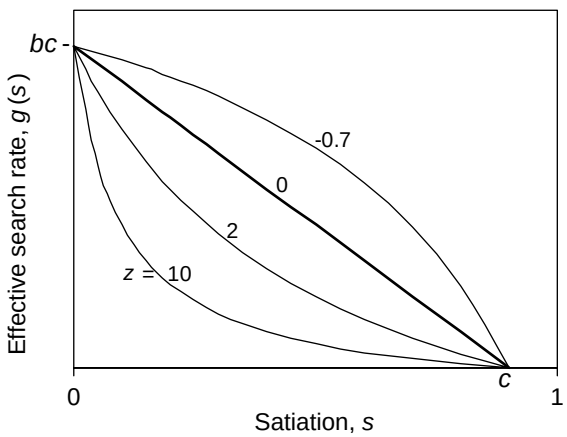

Fig. 1. Illustration of the function (Eq. 2) used to describe the effective search rate, g(s), in relation to satiation, s, for different values of the shape parameter z. The scaling parameter b and the capture threshold c are indicated along the axes.

captures can be modelled as point events associated with a jump in satiation level. The resulting probability distribution of satiation levels (p(s)) can be modelled by structured population models framed in partial differential equations that take ingestion jumps and gut clearing into account (Metz and Batenburg 1985a, b).

There are three types of events that affect the probability to end up at satiation level s:

- a net transition in s due to gut clearing,
- a transition away from s due to prey capture, and
- a transition (from $s-w$) to s by prey consumption.

These three events correspond with the three terms in the following model (Metz et al. 1988):

$$\frac{dp(s)}{dt} = -\frac{\partial asp(s)}{\partial s} - xg(s)p(s) + xg(s-w)p(s-w) \qquad (5a)$$

For satiation levels $s < w$ the last term equals zero. At satiation levels where $1-s \leq w$ prey capture will result in consumption to gut capacity ($s = 1$, where $g(1) = 0$):

$$\frac{dp(1)}{dt} = -\frac{\partial ap(1)}{\partial s} + \int_{1-w}^{1} xg(s)p(s)ds \qquad (5b)$$

Assuming that prey density changes at a much lower rate than the predator's satiation, the probability distribution of satiation, $\hat{p}(s)$, can now be assumed to be in a pseudo-steady state, which can be calculated for every value of x, by putting Eq. 5 equal to zero. (Metz et al. 1988 for calculation procedure). After normalising, so as to make the probabilities add up to unity, the mean functional response equals the $\hat{p}$-weighted average of Eq. 1:

$$F(x) = \int_{0}^{1} xg(s)\hat{p}(s)ds \qquad (6)$$

Knowledge on the steady state gut content can be used to relate female reproduction to prey density as well. Assuming that digested biomass is fully used for body maintenance (respiration and transpiration) and egg production, the following mass balance equation (at body level) should hold:

$$\tilde{a}Gs = mB + rE \qquad (7)$$

where G the gut capacity (in weight units), and $\tilde{a}$ the relative rate of digestion (close to the rate gut clearing), B the body mass, m the relative rate of respiration and transpiration, E is the weight of an egg, and r the rate of reproduction. If we define $\omega = \tilde{a}G/E$ (the conversion rate) and $\psi = mB/\tilde{a}G$ (the maintenance ratio), and assume that reproduction allocation will never be negative, the reproduction rate at satiation level s can be written as:

$$r(s) = \begin{cases} \omega(s-\psi) & \text{if positive} \\ 0 & \text{otherwise} \end{cases} \qquad (8a)$$

The mean oviposition rate within the predator population at prey density x now equals the p-weighted average of r(s) at prey density x:

$$R(x) = \int_{0}^{1} r(s)\hat{p}(s)ds \qquad (8b)$$

When the changes in satiation of individual predators are relatively fast compared to the assimilation rate, the individual reproductive response might be approximated on the basis of their mean satiation level ($\hat{s}$):

$$R(x) = r(\hat{s}(x)) \quad \text{where} \quad \hat{s}(x) = \int_{0}^{1} s\hat{p}(s)ds \qquad (8c)$$

The functional and numerical responses are now fully defined (by Eq. 5, 6, 8) and can be calculated numerically (Metz et al. 1988).

By making simplifying assumptions, more simple and explicit equations for the functional and numerical responses can be obtained. By assuming a balance between the biomass daily ingested from the captured prey and biomass daily cleared from the gut (both proportional to total gut capacity):

$$xg(\hat{s})w(\hat{s}) = a\hat{s} \qquad (9)$$

the steady state satiation, $\hat{s}$, may be solved for some explicit functions for g(s) and w(s). This value can then be used to calculate the functional and numerical responses from:

$$F(x) = xg(\hat{s}) \quad \text{and} \quad R(x) = r(\hat{s}) \qquad (10)$$

Building on this approach several limit-case approximations have been derived (Metz and Van Batenburg 1985a, b, Metz et al. 1988):

1) At very low densities, when satiation is close to zero:

$$F(x) = g(0)x = bcx \quad \text{and} \quad R(x) = 0 \qquad (11)$$

2) If prey content w_p is very small compared to the gut capacity of the predator, the satiation jumps are defined by the prey content and largely independent from the satiation level, so that approximately

$$w(s) = w_p \qquad (12)$$

Predation now results in minor satiation fluctuations, and approaches a continuous ingestion process. For the case that g(s) is linear ($z = 0$ in Eq. 2) this results (Appendix 1) in

$$F(x) = \frac{cax}{a + w_p bx} \text{ and}$$

$$R(x) = \omega\left(\frac{cw_p bx}{a + w_p bx} - \psi\right) \quad (13)$$

which is identical in shape to Holling's disk equation (Appendix 1).

3) If prey content w_p always exceeds the satiation deficit, so that

$$w(s) = 1 - s \quad (14)$$

but that nonetheless the mean level of satiation is close to its steady state value, the balance equation (Eq. 9) can also be solved for $\hat{s}$, resulting in quadratic expressions for F(x) and R(x) (Appendix 1).

4) If x is large enough to make satiation approach gut capacity, and every prey capture will result in full satiation, the time between prey captures will be dominated by the shape of the prey capture function g(s) near $s = c$, the capture threshold (Metz et al. 1988), resulting in

$$F(x) = a \times \left[\sqrt{\frac{a\pi}{2b'cx}} - \ln(c)\right]^{-1} \quad (15)$$

where b′, the slope of prey capture function (Eq. 2) near c (day^{-1}), is given by

$$b' = g'(c) = \frac{b}{1 + zc} \quad (16)$$

Neglecting variance, the expected biomass ingested per prey is equal to the biomass cleared from the gut during the expected time between prey captures (1/F(x)), so that

$$w(\hat{s}(x)) = 1 - e^{-a/F(x)} \quad (17)$$

Since from Eq. 9 and 10a it follows that

$$\hat{s}(x) = \frac{F(x)w(\hat{s}(x))}{a} \quad (18)$$

the numerical response (Eq. 10b) can be now described by:

$$R(x) = \omega\left[\frac{F(x)}{a}(1 - e^{-a/F(x)}) - \psi\right] \quad (19)$$

Experimental estimation of functions and parameters

The predatory mite *Neoseiulus barkeri* Hughes (=*N. mckenziei* Schuster & Pitchard) originated from the Glasshouse Research Station at Naaldwijk in the Netherlands, where it was reared with copra mites as prey (Ramakers 1983). In our laboratory this rearing was continued on other prey: spider mites and thrips on detached common bean leaves (*Phaseolus vulgaris* L.). The predatory mite *Neoseiulus cucumeris* (Oudemans) originated from Koppert BV (Berkel en Rodenrijs, the Netherlands), where it was reared on copra mites. In our laboratory it was reared on a diet of pollen of *Vicia fabae* in plastic arenas (Van Rijn and Tanigoshi 1999). The thrips *Frankliniella occidentalis* originated from the DLO-CPRO in Wageningen, the Netherlands, and was reared on potted *Chrysanthemum* plants in a climate box. The other prey species, *Thrips tabaci,* originated from the greenhouse of the biological centre of the University of Amsterdam, the Netherlands, and was reared on cucumber plants in a climate box.

For the experiments only gravid female predators were used. Females from *N. cucumeris* originated from cohorts that had been producing eggs for 2–5 days. Females from *N. barkeri* were not standardised in age, but to make sure that they were in the oviposition phase, they were selected based on the presence of a developing egg visible through the transparent body wall. The thrips larvae that served as prey were obtained from eggs that were laid three or more days earlier on detached cucumber leaves, placed upside down on moist cotton wool. Since capture success is strongly affected by prey size (Van der Hoeven and Van Rijn 1990), the larvae selected for the experiments were standardised in size: 0.4–0.5 mm for *Thrips tabaci* and 0.5 to 0.6 mm for *Frankliniella occidentalis.*

Gut content and rate of gut clearing

The maximum gut content (G) was determined as the weight increase of a 48 h starved mite after feeding on a thrips larva large enough to satiate the predator (experiment 1). The weight was assessed by an electronic microbalance (Sartorius® Supermicro S4) with a precision of 0.1 µg. Individual predators were anaesthetised with carbon dioxide before they were transferred from the leaf disk to the weight balance.

It was assumed that the gut is emptied in an exponential fashion (Holling 1966, Sabelis 1986). The rate of gut clearing (a) was shown to be only 5% lower than the rate of digestion (ã) (Sabelis 1986). The rate of digestion was estimated indirectly, by assuming a balance between biomass intake from the gut on the one hand and the biomass use for egg production, transpiration and respiration on the other hand (Eq. 7) and by measuring the remaining parameters of this balance equation.

The rate of respiration and transpiration (m) was estimated by determining the weight decrease during starvation (experiment 2). To this end, individual mites (directly obtained from the culture) were weighed after a deprivation period of 0, 6, 24 and 48 h, during which

they were kept individually in small capsules with a gauze-covered opening at 25°C and 85% RH. The resulting time series were fitted by:

$$W(t) = Be^{-mt} \quad (20)$$

where W represents the body weight minus the weight of the eggs produced by that female during the experiment (number of eggs times E, the weight of an egg). Note that oviposition occurred only during the first day of starvation.

To complete the information needed for calculating the predator's mass balance, the oviposition rate was assessed as the highest mean rate observed in experiments to determine the numerical response to a range of prey densities. The corresponding mean satiation level (s) was calculated (close to 0.8) using the predation model (Eq. 5, 6, 8). This involved an iterative procedure to tune the parameter a, such that both the oviposition rate and the prey capture function matched the observations at the specific prey density.

Search rate

The effective search (or 'prey capture') rate (g) can be decomposed in search rate (u) and capture success upon encounter (k), all of which depend on the satiation level (s):

$$g(s) = u(s) \times k(s) \quad (21)$$

Assuming random walk, the search rate (u, the leaf surface crossed per unit of time) equals the mean resultant displacement of predator and prey (V) times the width of the searching path (d) (Sabelis 1986):

$$u = V \times d$$

When walking directions of predator and prey are independent, the resultant displacement is given by the vector sum of the walking velocities of predator and prey (Skellam 1951):

$$V = \sqrt{V_p^2 + V_n^2}$$

Since thrips walking velocity is less than 20% of that of the predator (since most of the time it is not moving at all), the prey contributes less than 4% to the resultant displacement and prey movement can therefore be ignored. The predator's walking velocity (V_p) can be decomposed in walking speed (in periods of ambulatory activity) (v_p) times proportion of time spent walking (f_p).

Walking activity of the predator (f_p) in the presence of prey was recorded during the experiments to measure the capture success ratio (below), whereas walking activity in the absence of prey was estimated in a separate experiment. Here, ca 30 female predators were distributed over 10 cucumber leaf disks of 20 cm^2 each, floating upside down on watersoaked cotton wool. The disks had been fed upon by five thrips larvae during one day after which they were removed. Predators, directly taken from the culture or starved for three hours, were introduced and the number of actives were recorded visually, every 20 min.

Walking speed of the predator (v_p) was recorded by time-lapse video (2 images s^{-1}) through a binocular microscope, leading to 20 × magnification on the video screen. The position of an active predator on the video screen was marked every 5 s and the distances between successive marks were measured.

Lateral reach of the active predator (d_p) is determined by tactile perception of prey with sensors on the front legs that swing alternatingly to the left and to the right (Sabelis 1986). The maximum angle between front leg and body axis (φ), the length of the front legs (l, distance between dorsal shield and leg tip, measured only when image was sharp) and the distance between their bases (d) was determined from frame-by-frame displays (at 80 × magnification) of the video records (50 images s^{-1}). Using mean parameter values the lateral reach was calculated from $d_p = d + 2l\sin\varphi$ (Takafuji and Chant 1976).

The width of the searching path equals the lateral reach of the predator's front leg (d_p) plus the mean diameter of the prey (d_n). As predators approach a prey at a random angle, the mean diameter of the prey (d_n) was taken to be half the sum of its length and width. The size dimension of living thrips, including extremities such as antennae and legs, were measured using a binocular (at 25 × magnification) provided with a metric scale.

The search rate of the predator was finally calculated as:

$$u = f_p \times v_p \times (d_n + d_p) \quad (22)$$

using the parameter estimates obtained from the procedures above. If necessary, dependence on satiation was incorporated.

Capture success, encounter rate and prey handling time

Capture success (k) was assessed for predators that experienced different starvation periods prior to the test and hence had different satiation levels. A few hours before the trial, a cucumber leaf disk (var. Corona or Ventura) of five cm^2 was infested with 20 thrips larvae. The predator was introduced to the leaf disk via the opened plastic vial used for food and water deprivation. As soon the predator moved out, the vial was removed and the trial started. All encounters between predator and prey were recorded. The trial ended when a larva was consumed, or when either 45 min or 30 encounters passed. For each satiation level, the capture success ratio was calculated as the total number of trials that ended by

predation divided by the number of encounters observed in all trials. Prey handling time was recorded as the period between prey capture and final abandonment of the prey. The food content of a thrips larva was estimated as the difference in weight between prey remnants left by two-day-starved predators and live specimens.

To enable an independent test of the search rate (u), the expected rate of prey encounter, which equals search rate times thrips density (u.x), was compared with the rate of prey encounter observed in the capture success experiments. The numbers of encounters observed during the experiments were added up for mites with similar satiation levels and divided by the total observation time. Trials with less than three encounters were excluded.

Validation experiments

Rates of predation and oviposition were determined experimentally for two combinations of predator and prey: *Neoseiulus barkeri* with *Thrips tabaci* and *Neoseiulus cucumeris* with *Frankliniella occidentalis*. One predatory mite and a fixed number of thrips larvae were put together on a leaf disk for three days. To ensure that the total number of larvae per disk never dropped below 50% of the initial number, the disks were checked for dead and live prey twice a day (for *N. cucumeris*) or every eight hours (for *N. barkeri*) and dead, as well as too large live, thrips larvae were removed and replaced by fresh prey. Only at thrips densities larger than 1 cm^{-2}, unacceptable damage to the leaf was prevented by refreshing the leaf disk once a day. The different prey densities studied were obtained by varying the initial numbers of thrips larvae and the area of leaf disks (cm^2) in the following ratios: 5/20, 10/10, 20/20 and 20/4 for *Neoseiulus barkeri*, and 8/120, 10/25 and 12/4.5 for *Neoseiulus cucumeris*. For each prey density the experiments were replicated 10–15 times. The effective prey density was defined as half the sum of the initial prey density and the mean prey density observed after each experimental period.

The fit between model predictions and direct measurements were evaluated graphically, as well as by the application of a lack-of-fit F-test (Draper and Smith 1966). For this test the residual variance is spit into the 'pure error' variance (MS_{PE}) resulting from spread in replicate measurements around their mean at each prey density, and the 'lack-of-fit' variance (MS_{LOF}) resulting from the deviations between mean values and model predictions. The null hypothesis that the model is adequate is rejected when MS_{LOF} is significantly greater than MS_{PE}. Under the null hypothesis the ratio

$$F_0 = \frac{MS_{LOF}}{MS_{PE}}$$

follows an F distribution with m-p and n-m degrees of freedom for numerator and denominator respectively, where n is the total number of replicate measurements, m the number of (prey density) levels studied, and p the number of unknown parameters in the model. With respect to predation rate $p=0$, as all parameters have been estimated on the basis of independent measurements. With respect to oviposition rate $p=1$, as one parameter (a, the rate of gut clearing) have been estimated on basis of the oviposition data.

Predictions and validation

Gut content and rate of gut clearing

Estimates of the parameters in the mass balance equation (Eq. 7) are given in Table 1. Compared to *N. barkeri*, *N. cucumeris* has a larger net body mass (B), maximum gut content (G) and egg size (E). The relative rate of respiration and transpiration (m), however, is similar for both species (Fig. 2). According to Van Rijn and Van Houten (1991), oviposition rates of the two predator species are equal. However, compared to *N. cucumeris* the mean age of *N. barkeri* females used in our experiments was higher, which explains why their mean oviposition rate (Fig. 4B) was lower. For the same reason, the rate of digestion (ã), derived from the mass balance equation (Eq. 7), and consequently, the rate of gut clearing ($a = \tilde{a}/0.95$), are lower for *N. barkeri* as well (Table 1).

Search rate

Estimates of the parameters in the equation for the search rate (Eq. 22) are given below.

Walking activity (f). In the absence of thrips larvae, walking activity of *N. cucumeris* initially decreased after release on the leaf disks and reached a stable level of ca

Table 1. Weights and rates (mean ± standard deviation, n = 9–12) of adult female predators.

Species	Egg weight E (μg)	Net body weight B (μg)	Rate of respiration and transpiration m (day^{-1})	Maximum gut capacity G (μg)	Rate of gut clearing[1] a (day^{-1})
N. barkeri	2.05 ± 0.26	9.94 ± 1.0	0.243 ± 0.027	3.8 ± 0.2	1.65
N. cucumeris	2.15 ± 0.07	12.2 ± 1.2	0.256 ± 0.022	5.2 ± 0.8	2.40

[1]Calculated from body mass balance Eq. 7, assuming that $a = \tilde{a}/0.95$.

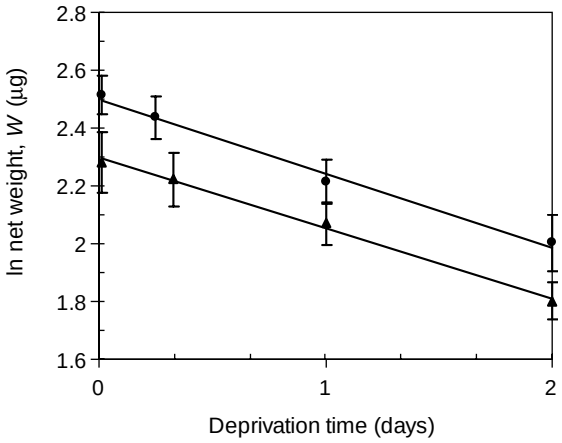

Fig. 2. Weight loss during starvation (at 25°C and 85% RH). Net weight (W) is calculated per female predator by taking the actual body weight minus the weight of the eggs produced afterwards. Symbols and error bars indicate the log mean net weight and its 95% confidence interval: triangles for *Neoseiulus barkeri* and dots for *N. cucumeris.* The relative rate of respiration and transpiration (m) is estimated by the mean slope of the regression lines (Eq. 20; 0.243 day^{-1} for *N. barkeri* and 0.256 day^{-1} for *N. cucumeris*.) The maximum net body weight (B) equals (the exponent of) the intercepts (9.94 and 12.2 µg respectively).

0.39 after ca 4 h, both in mites that had and had not experienced a 3 h period of starvation before release (data not shown). This suggests that the activity is not related to the level of satiation. The average over the first three hours is comparable with the 0.65 reported by Peterson (1990, Ch. 2) who observed 24 h starved mites, during three hours after release, also in absence of thrips. In the presence of thrips larvae, activity of predatory mites did not change consistently with the starvation period either and was on average 0.74 for *N. barkeri* and 0.73 for *N. cucumeris* (Fig. 3A). Evidently, the presence of thrips activates the predator to a similar level at all satiation levels.

Walking speed (v_p) in absence of thrips, but in presence of thrips-inflicted leaf damage, seems to be maximal at intermediate satiation levels (Fig. 3B). However, the difference between satiation levels is clearly not significant ($F = 0.101$, $df = 8,59$, $P = 0.99$), and walking speed is therefore taken to be constant: 0.42 mm s^{-1} for *N. barkeri* and 0.44 mm s^{-1} for *N. cucumeris*. These values are only slightly lower than the 0.56 mm s^{-1} reported by Peterson (1990, Ch. 2) for 24 h starved *N. cucumeris* in absence of thrips. We did not observe obvious differences in walking speed between predators on thrips-damaged leaf disks or leaf disks with thrips larvae present, and assumed walking speed to be independent of prey presence. (The validity of this assumption is confirmed by the results on the rate of prey encounter; next paragraph.)

Width of searching path ($d_p + d_n$). The length of the front legs (l), as well as the maximum angle between front leg and body axis during search (φ), appear to be larger for *N. barkeri* than for *N. cucumeris,* resulting in a wider lateral reach (d_p) of the former predator (Table 2a). The resulting width of the searching path, i. e. lateral reach (d_p) plus the mean prey diameter (d_n, Table 2b) is 1.03 mm for the combination *N. barkeri – T. tabaci*, and 0.98 mm for the combination *N. cucumeris – F. occidentalis*.

Since all parameters in the search rate equation (Eq. 22) appear to be independent of the satiation level, the estimated search rate (u) is a constant as well, and virtually equal for the two combinations: 0.311 $mm^2\ s^{-1}$ (or 269 $cm^2\ day^{-1}$) for *N. barkeri* foraging on *T. tabaci*, and 0.310 $mm^2\ s^{-1}$ (or 268 $cm^2\ day^{-1}$) for *N. cucumeris* foraging on *F. occidentalis*.

Validation of the rate of prey encounter

The mean rate of prey encounter is expected to equal search rate times thrips density ($u \times x$) and, based on the aforementioned conclusions, is expected not to change with satiation. The validation test (at a prey density of 4 cm^{-2}) showed no significant deviations between predictions and observations for *N. barkeri*, although on average the observations were higher than predicted (Fig. 3C). For *N. cucumeris*, however, the observations were below the predicted rate (Fig. 3C). In agreement with the expectations no effect of satiation was observed. These results also suggest that the presence of thrips larvae (as in these encounter rate experiments) has no major effect on the search rate as compared to the presence of thrips-inflicted leaf damage only (as in the walking speed experiments).

Capture success and prey capture function

Given the observed constancy of the search rate ($u(s) = u$), satiation (s) will only affect prey capture rate by affecting capture success (k, the probability of successful capture upon encounter), since $g(s) = u \times k(s)$. Fitting the capture success data by the function that is also used to describe prey capture, g(s) (Eq. 2, albeit with a different scaling parameter: b_k instead of b), we directly obtain the parameter estimates of the prey capture function (with $b = u \times b_k$).

The highest capture success ratios are observed at low satiation levels (Fig. 3D): ca 0.55 for *N. barkeri* and 0.32 for *N. cucumeris*. For *N. barkeri* the drop in k occurred above satiation $s > 0.5$, whereas for *N. cucumeris* k immediately declined for $s > 0$. Predictions from the predation model are particularly sensitive for the capture threshold (c), the level of satiation at which the capture success and consequently the prey capture function becomes zero. Different estimates were obtained by fitting three variants of Eq. 2 (with b_k rather than b)

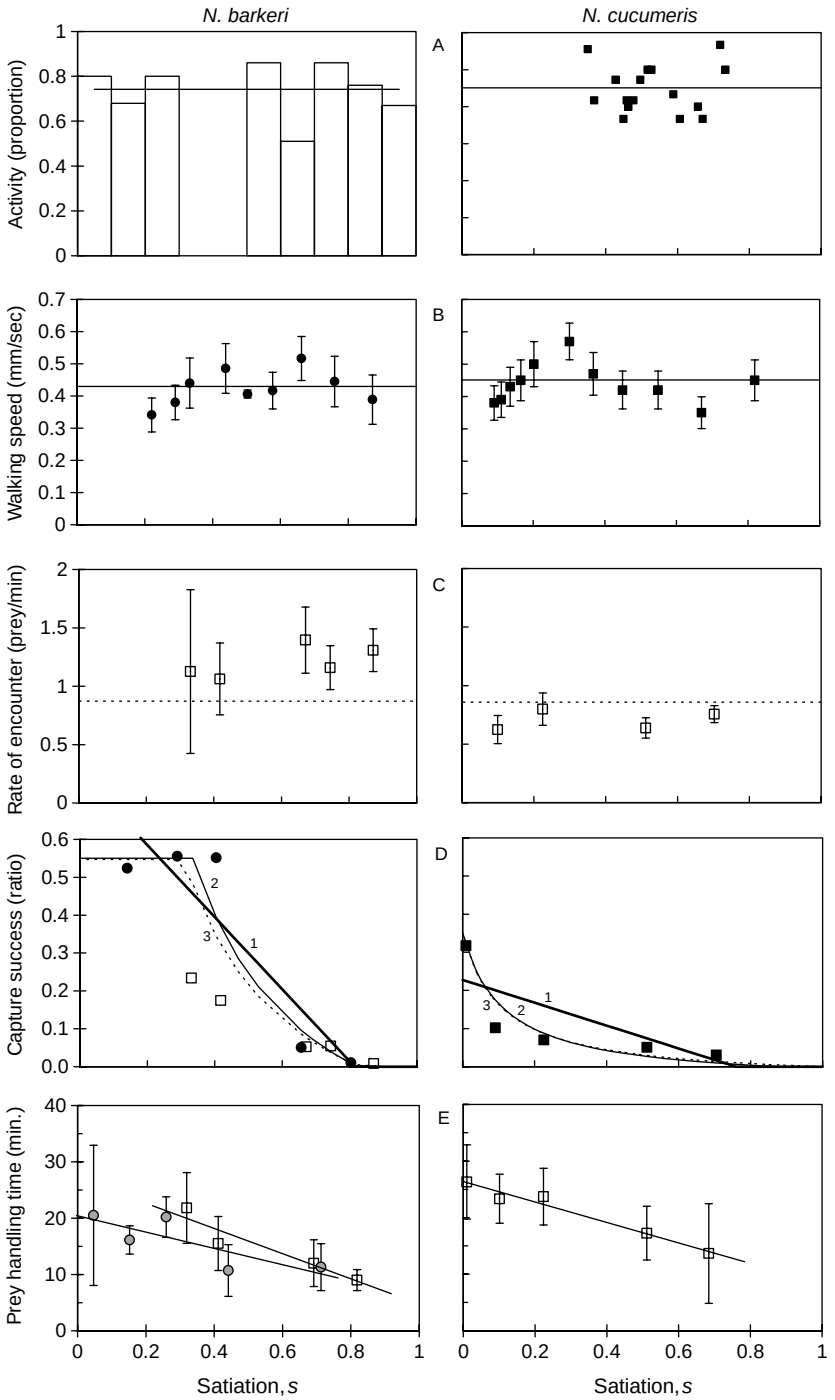

Fig. 3. Foraging parameters in relation to satiation for *Neoseiulus barkeri* (left) and *Neoseiulus cucumeris* (right): (A) walking activity, (B) walking speed, (C) predicted (lines) vs observed (symbols) prey encounter rates ($u \times x$) with $x = 4$ larvae cm^{-2}, (D) capture success ratio (k), and (E) prey handling time. Data points are fitted by a constant (A, B) or a linear function (E). The capture success ratios (D) are fitted by Eq. 2, replacing b by b_k (the maximum capture success ratio) with different constrains that result in different models (see text and Table 3): linear model 1 (thick line), convex model 2 (drawn thin line) and convex model 3 (dashed line). Closed symbols indicate data used for model parameterization. Dots represent data with *T. tabaci* as prey, squares data with *Frankliniella occidentalis* as prey.

Table 2a. Predator dimensions in mm (mean ± standard deviation, n = 10–15).

Species	Body length	Width 1st leg base (d)	Length 1st leg (l)	Max. angle–body axes (φ)	Lateral reach $d_p = d + 2l \sin\varphi$
N. barkeri	0.37 ± 0.02	0.08 ± 0.01	0.32 ± 0.01	57° ± 5°	0.61
N. cucumeris	0.38 ± 0.01	0.09 ± 0.01	0.27 ± 0.01	50° ± 6°	0.51

Table 2b. Size and weight of thrips larvae (mean, n = 9–11).

Species	Length class (mm, ex. antennae)	Size (mm)			Weight (μg)			Food content rel. to G (w_p)[1]
		Length (incl. antennae)	Width (incl. legs)	Mean diameter (d_n)	Fresh weight	After full ingestion	Food content	
T. tabaci	0.44–0.55	0.61	0.24	0.42	4.5	1.7	2.8	0.74
F. occidentalis	0.50–0.60	0.66	0.28	0.47	5.8	1.8	4.0	0.77

[1]G (gut capacity) of predators *N. barkeri* and *N. cucumeris* respectively.

to the observed data (minimising sum of squared relative deviations):

1) a linear non-negative function in s (b_k or c to be fitted, z = 0), forced through the data point that is associated with the highest satiation (s) level,
2) a nonlinear function with c fixed at the mean of the estimates obtained from variants (1) and (3) (b and z to be fitted),
3) a nonlinear function without constraints (z, c and b_k to be fitted).

The parameter values that minimize the proportional difference between function values and data points are shown in Table 3, and the resulting curves in Fig. 3D. The nonlinear (convex) variants give a better fit to the data (two-fold, when corrected for the degrees of freedom) but the linear variant clearly benefit from simplicity.

Prey handling time

With *F. occidentalis* as prey, the mean period between prey capture and prey abandonment varies from ca 10 minutes for nearly satiated predators to ca 30 min for starved predators, and appear to be similar for both predator species (Fig. 3E). Regarding the smaller *T. tabaci* as prey, handling time seems to be somewhat shorter (no testing possible).

At high prey densities *N. cucumeris* captures ca 6 prey per day (Fig. $4A_2$), and spend (due to high satiation levels) about 10 min on each prey. The total handling time of 60 min per day is only 4% of their total time budget. At the lowest of our experimental prey densities the predation rate is ca 4 per day and (with an estimated mean satiation of 70%) the mean handling time is ca 12 min per prey (Fig. 3E), resulting in a total prey handling time of 48 min per day. When lowering the prey density even further, the predation rate goes down faster than the time spent handling one prey, and the total prey handling time will consequently decrease to even lower levels. Thus, for this system handling time can safely be ignored when calculating predation rates.

Predation and oviposition rates: predictions vs observations

The observed functional responses show all qualitative characteristics of a Holling type 2 response (Fig. 4A). The observed predation rates reach a plateau for *N. barkeri* above 1 thrips larva per cm^2 and for *N. cucumeris* above 0.25 thrips larvae per cm^2. The observed numerical responses seem to reach a plateau at even lower prey densities, especially for *N. cucumeris*, and there seems to be even a small decline at the highest prey density. However, this decline is likely to be due to thrips larvae consuming predator eggs, a phenomenon recently discovered (Janssen et al. 2002), which will only be important when thrips density is high. For this reason, we used the oviposition rate at the intermediate rather than at the highest prey density to parameterise the mass balance equation (Eq. 7).

Table 3. Parameter estimations of the prey capture function g(s) (= u × k(s)), based on capture success data.[1] See also Fig. 3D.

Predator – prey system: Parameter		*N. barkeri–T. tabaci*			*N. cucumeris–F. occidentalis*		
	Set no.	1[2]	2[3]	3[3]	1	2	3
Shape parameter	z (–)	0	1093	1282	0	8.69	9.24
Capture threshold	c (–)	0.815	**0.822**	0.829	0.76	**0.88**	1
Scale parameter	b_k (–)	0.95	418	421	0.30	0.40	0.35
Lack-of-fit (proportional)							
Sum of squares	SS_{LOF}	4.00	0.91	0.63	3.06	1.26	1.02
Levels – parameters (m–p)	df	5–2	5–3.5	5–4	5–2	5–2.5	5–3
Mean square (variance)	MS_{LOF}	1.33	0.61	0.63	1.02	0.50	0.51

[1]since the prey capture function g(s) = u × k(s), the capture success k(s) can be described by the same function (2), provided that b [cm^2 day^{-1}] is replaced by a nondimensional b_k representing the maximum capture success ratio. b can later be computed as: $b = u \times b_k$, where u = 269 and 268 cm^2 day^{-1} for the two systems respectively.
[2]bold parameter values are fixed, while other parameters are chosen freely to minimise the sum of squares SS_{LOF}.
[3]k(s) function maximised at k = 0.55 (adding a fourth parameter to the capture success [and prey capture] function).

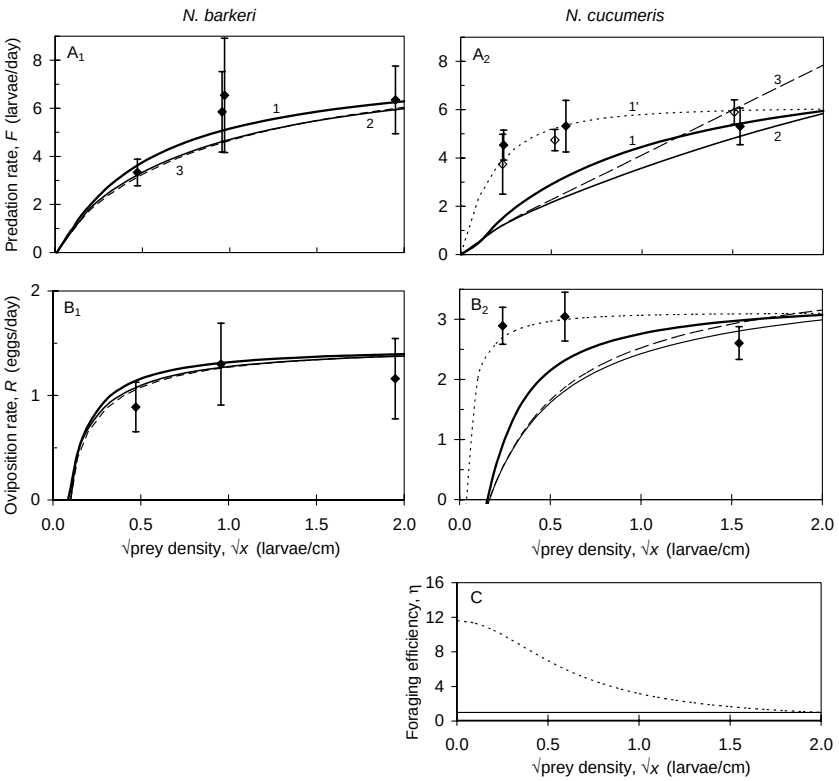

Fig. 4. Functional and numerical response. Predicted (lines) vs measured (symbols) rates of predation (A) and oviposition (B) in relation to (the square root of) prey density x. Left panels: *Neoseiulus barkeri* with *Thrips tabaci* (0.44–0.55 mm) as prey; right panels: *Neoseiulus cucumeris* with *Frankliniella occidentalis* (0.5–0.6 mm) as prey. Symbols indicate means of 10–15 replicates. Vertical bars represent 95%-confidence intervals. Open symbols indicate results from experiments where prey on leaf disks has been replaced once rather than twice a day. Drawn lines indicate predictions from the full predation model (defined by Eq. 5, 6, 8 and parameter values shown in Table 4) using either a linear (model 1, thick line) or one of the convex prey capture functions (model 2: drawn thin line; model 3: dashed line). Dotted lines show the model predictions of the model (1') in which the rate of effective search is multiplied with a foraging efficiency factor (shown in C) that decreases with prey density (x) according $\eta(x) = \eta_0/(qx+1)$. The parameters $\eta_0 = 11.6$ and $q = 2.65$ cm^2, are chosen to equal one at $x = 4$ cm^2 and to minimize the squared deviations between model predictions and experimental results for predation rate (*N. cucumeris* only).

The functional and numerical responses predicted by our model (defined by Eq. 5a, 5b, 6, 8a, 8b) for the different parameter sets summarized in Table 4, are shown in Fig. 4A and 4B. The independent model predictions matched observations for *N. barkeri* feeding on *T. tabaci* reasonably well, irrespective of prey capture function estimates used (also indicated by non-significant lack-of fit statistics, Table 4). However, for *N. cucumeris* feeding on *F. occidentalis* a good match was only obtained at the highest prey density (4 cm^{-2}). At lower prey densities the predation and oviposition rates observed were much higher than predicted (especially when using the nonlinear prey capture function estimates, sets 2 and 3, Table 4). This indicates that the model does not sufficiently capture the predation process at low prey densities.

Comparison of the experimental results with published data showed reasonable correspondence with respect to the plateau levels of the functional responses (Sabelis and Van Rijn 1997). For *N. cucumeris*, our estimate of the consumption rate (5–6 flower thrips larvae day^{-1}) was close to those reported in the literature (same temperature, same host plant): 4.0–4.7 (Peterson 1990), 6.0 (Van Houten et al. 1995) and 6.9 larvae day^{-1} (Shipp and Whitfield 1991; note that they used dead, defenceless prey!). For *N. barkeri*, our estimate (6 onion thrips larvae day^{-1}) was somewhat higher than reported (same temperature, but other host plant, bean): 4.3 larvae day^{-1} (Bonde 1989). Plateau levels of the numerical response of young females of *N. cucumeris* (3 eggs day^{-1}) are higher than reported in the literature: 1.9 eggs day^{-1} Castagnoli et al. (1990) and 2.2 eggs day^{-1} (Van Houten et al. 1995). However, those of *N. barkeri* females (all ages) (1.2 eggs day^{-1}) were lower than the reported 2.3 (Bonde 1989) and 1.9 (Momen 1996) eggs day^{-1}.

Reports on the rising part of the functional response show a much more gradual increase with prey density (Peterson 1990, Shipp and Whitfield 1991), which likely results from the absence of an adaptation period preceding and adequate prey replacement during the predation measurements.

Sensitivity analysis

Sensitivity of the model output to changes in input parameters is evaluated in Fig. 5. This evaluation shows that at high prey densities predation rates are mostly affected by the capture threshold (c) and the rate of gut clearing (a), whereas at low prey densities predation rate is more sensitive to variation in the effective search rate

Table 4. Goodness-of-fit of the satiation driven predation model to predation and oviposition rate measurements for different sets of prey capture parameters (Table 3, Fig. 4).

Predator – prey system:		*N. barkeri–T. tabaci*			*N. cucumeris–F. occidentalis*		
Model parameters							
Rate of gut clearing	a (day^{-1})		1.65			2.4	
Prey content	w_p (–)		0.74			0.77	
Conversion rate (day^{-1})	ω (day^{-1})		2.91			5.51	
Maintenance ratio	ψ (–)		0.406			0.263	
Prey capture function, g(s)	no.	1	2	3	1	2	3
Shape parameter	z (–)	0	1093	1282	0	8.69	9.24
Capture threshold	c (–)	0.815	0.822	0.829	0.76	0.88	1
Scale parameter	b ($cm^2\ day^{-1}$)	255.7	112 489	113 296	80.3	106.6	93.8
Slope at s = c	b′ ($cm^2\ day^{-1}$)	255.7	125.1	106.5	80.3	12.3	9.2
Predation rate, lack-of-fit statistics							
Lack-of-fit variance	MS_{LOF}	0.64	1.42	1.52	3.68	7.93	7.8
Pure error variance	MS_{PE}		6.58			1.78	
	F_0	0.098	1.422	1.522	2.07	4.45	4.38
	df		4, 43			3, 28	
	P	0.98	0.93	0.92	0.13	**0.011**	**0.012**
After correction with foraging efficiency factor η (*N. cucumeris* only):							
	F_0				0.21	1.23	1.91
	df					2, 28	
	P				0.81	0.31	0.17
Oviposition rate, lack-of-fit statistics							
Lack-of-fit variance	MS_{LOF}	0.680	0.043	0.040	1.93	7.16	7.29
Pure error variance	MS_{PE}		0.365			0.309	
	F_0	1.86	0.117	0.109	6.24	23.2	23.6
	df		2, 35			1, 19	
	P	0.17	0.89	0.90	**0.022**	**0.0001**	**0.0001**
After correction with foraging efficiency factor η (*N. cucumeris* only):							
	F_0				0.02	0.22	0.15
	df					1, 19	
	P				0.90	0.65	0.70

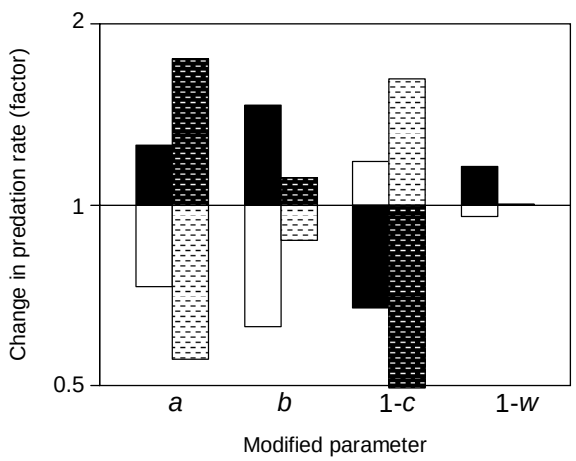

Fig. 5. Sensitivity analysis: the effect on prey consumption rate (presented on a log scale) at low prey densities (0.1 cm^{-2}, no pattern) and high prey densities (4 cm^{-2}, punctured) of a 2-fold increase (black bars) or decrease (white bars) in parameter values for: rate of gut clearing (a), maximum effective search rate (b), the capture threshold (expressed as satiation deficit, 1-c), and the prey content relative to the maximum content of the gut (w_p), using the default parameter values for *N. cucumeris* (a = 2.4 day^{-1}, z = 0, b = 80.3 $cm^2\ day^{-1}$, c = 0.76, w_p = 0.77). Horizontal lines indicate a 2-fold increase or decrease in prey consumption rate.

(b). The input parameters affect the predation rate either proportionally (in case of the capture threshold) or (much) less than proportionally. Since we believe errors in parameter estimations to be less than a factor 2, we conclude that the difference between observations and predictions for *N. cucumeris* at low thrips densities cannot be due to errors in the inputs.

Model approximations

The different approximations for the stochastic predation model, as presented in the model section (Eq. 11–19), vary strongly in the range of prey densities for which it accurately describes the expected functional response (Eq. 5, 6) properly (Fig. 6A). The zero-satiation approximation (1, Eq. 11) clearly only holds for very low prey densities. The small prey approximation (2, the satiation version of Holling's disk equation, Eq. 13) is clearly not valid for our system as well. For the large prey (high w_p value) the functional response is levelling off much too soon, as mean satiation is expected to reach its maximum much too soon. The large prey approximation (3, Appendix 1, Eq. A10) does a much better job, although it overestimates the prey consumption rate generally with 10–25%. Metz' approximation (4, Eq. 15)

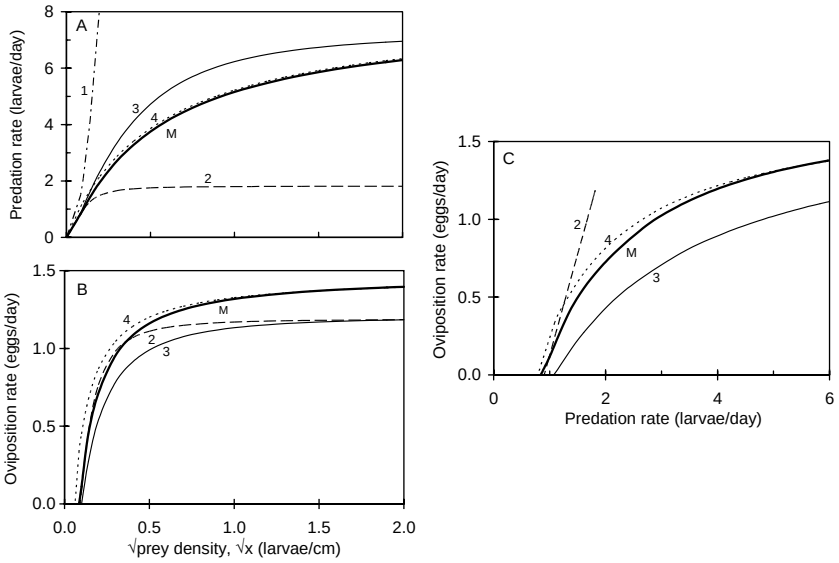

Fig. 6. Predictions for the functional response (A), the numerical response (B), and its interrelationship (C) by (M) the full stochastic model (Eq. 5, 6, 8) (thick line) and four of its approximations: (1) zero satiation (Eq. 11, dash-dotted line), (2) small prey content (Eq. 13, dashed line), (3) large prey content (Eq. A10, A13, thin line), and (4) Metz' approximation (Eq. 15 and 19, dotted line). Parameter values for *N. barkeri* as given in Table 4 for the linear prey capture function (set 1) ($z=0$, $a=1.65$ day^{-1}, $b=256$ cm^2 day^{-1}, $c=0.815$, $w_p=0.74$, $\omega=2.91$ day^{-1}, $\psi=0.406$).

for the stochastic predation model is surprisingly accurate for the given set of parameters. The prey consumption rate is overestimated by more than 5% only when prey density falls below ca 0.2 cm^{-2} (Fig. 6A).

The functional response and the numerical response are related by linear conversion only under the small-prey assumption (approximation 2, Fig. 6B, C). Since the prey content in our system is relatively large compared to gut capacity of the predator (74%), the prey is generally only partially consumed. This results in a food intake rate, and consequently, an oviposition rate that levels off at higher predation rates. This property of the full predation model is captured both by the large-prey approximation (3, Eq. A13) and by Metz' approximation (4, Eq. 19), but most accurately by the last one (Fig. 6C). This property can indeed be observed in many experimentally established relationships between oviposition and prey consumption of arthropod predators (Beddington et al. 1976, Hayes 1988, Momen 1996, Nwilene and Nachman 1996b, Castagnoli and Simoni 1999, Agarwala et al. 2001).

Discussion

Based on experimental validation of the predation model, satiation-driven behaviour explains the predation rate observed for *N. barkeri* at all densities of *T. tabaci*, but for *N. cucumeris* feeding on *F. occidentalis*, only at the highest density, i. e. close to the conditions under which the parameters were estimated. At all other, i. e. lower, prey densities, *N. cucumeris* showed much higher predation and oviposition rates than predicted. This difference appears to be too large to be explained by parameter errors, even when assuming them to be of order 2. Hence, we conclude that here the effect of prey density on predation is not exclusively explained by the impact of satiation. We hypothesise that it is a consequence of the prey environment influencing behaviour in a way that is independent of satiation: apparently, the predator (with a given satiation level) forages much more efficiently at lower than at higher prey densities. To illustrate this point we introduced a foraging efficiency factor into the predation model that declines asymptotically with prey densities, but equals unity at the density of the parameterisation experiments (4 cm^{-2}; Fig. 4C). This showed that at low prey densities the foraging efficiency has to increase 12 fold to obtain a good fit between model and observations (Fig. 4C, Table 4). This increase in foraging efficiency at low prey density can be achieved either by nonrandom search, increased search rate, increased capture success, or a combination of these behavioural components. Below, we discuss these possibilities, identify different mechanisms and outline experimental tests to discriminate between them.

Nonrandom search

Plant-inhabiting predatory arthropods are known to increase their foraging efficiency by various modes of nonrandom search (Sabelis 1992): (1) increased turning rate after contact with prey and their products (faeces, feeding traces, etc.; e.g. Heimpel and Houghgoldstein 1994, Monyaneza and Obrycki 1998), (2) orientation to prey volatiles (alarm, aggregation or sex pheromones; Kielty et al. 1996, Boo et al. 1998, Haynes and Yeargan 1999, Mondor and Roitberg 2000) or herbivore-induced plant volatiles (Dicke and Sabelis 1988, Dicke 1999), and (3) release of marks (faeces, nonvolatile pheromones) to help avoid (retrieve) a site void of (occupied by) prey (Sheehan et al. 1993, Bernstein and Driessen 1996).

In general, predatory mites exhibit all three mechanisms (Sabelis and Dicke 1985) and there is even supporting evidence for the case of *N. cucumeris*. This predator showed increased turning rates and decreased walking speed after contacting leaf areas damaged by *F. occidentalis* (Peterson 1990). In addition, *N. cucumeris* responds olfactorily to chemical substances (decyl and dodecyl acetate) constituting the alarm pheromone of *F. occidentalis* (Teerling et al. 1993a) or to thrips-induced plant volatiles (Janssen et al. 1998). Future experiments should elucidate which mode of nonrandom search is particularly relevant at low prey densities at the given spatial scale, and to what extent it explains the increased foraging efficiency detected by our analysis.

Search rate decreasing with prey density

The rate of prey encounter at low prey densities can also be promoted by factors other than directed search: walking activity and walking speed. Our behavioural experiments carried out at high prey density did not show a relation of these factors with satiation, but this relation may change (in level or slope) had the experiments been carried out at low prey densities. Actually, there are many reports on arthropod predators, showing that search rate decrease with increasing prey density (Eveleigh and Chant 1981, Monyaneza and Obrycki 1998, Hirvonen 1999, Stewart et al. 2002). In these experimental studies, however, the phenomena can both be explained by an effect on satiation alone or by a direct effect of prey density alone, and further studies are required to separate the effect of prey density via satiation from other, more direct, effects of prey density.

Capture success decreasing with prey density

The underestimation of the predation rate of *N. cucumeris* at low prey densities may also be the result of an underestimated capture success at low prey densities. In the model it is assumed that capture success is only affected by prey density via satiation, but it is possible that prey density has an effect of capture success independent from satiation. Since even at low satiation levels the mean capture success of *N. cucumeris* is never higher than 0.33 there is clear room for improvement. Such increased mean capture success at low prey densities, even at constant satiation levels, is actually expected from theory on optimal foraging for variable prey (OFT, Charnov 1976). Small changes in prey size are known to affect capture success greatly (Van der Hoeven and Van Rijn 1990), but despite our effort to standardize the prey, some variation in size had to be accepted (The sizes of the thrips larvae ranged from 0.5 to 0.6 mm initially, but this range slightly increased during the 12 h intervals due to differential growth of male and female larvae). OFT now predicts that when prey differs in size, the predator should feed on the most profitable only when prey is abundant, but should be much less selective when prey becomes scarce. In experiments where only the overall ratios of captures over encounters are registered this would show up as a low capture success at high prey densities and much higher capture success ratios at low prey densities. Such changes in capture success have been reported in the literature (Hirvonen and Ranta 1996), but again it is not clear whether they indicate an effect of satiation alone or an other, more direct, effect of prey density.

Another way in which a direct effect of prey density may be manifested is through a confusion effect at high prey density, as reported for another prey–predatory mite interaction by Mori (1969). For our predator–prey system this is a possible mechanism as well, since attack on a given thrips larva often results in increased activity of other thrips larvae nearby, probably due to the release of an alarm pheromone (Teerling et al, 1993b) and active defence responses by the larva by jerking its abdomen and producing droplets of rectal fluid (Bakker and Sabelis, 1989). At high prey density, the high frequency of being hit by thrips larvae (or perception of the pheromone) may trigger 'confusion' in the predatory mite, resulting in encounters that are not ensued by capture attempts. At low prey densities such confusion will not likely occur, thereby providing another explanation for the higher than predicted predation rate.

How to improve studies on arthropod predatory behaviour?

We showed that for *N. barkeri* the steady state predation rate can be explained from experimentally established relations between satiation and foraging behaviour alone. However, this was not possible for *N. cucumeris*, in particular at prey densities lower than the one at which the satiation-behaviour relationship was assessed. The recognition of such deviations between predicted and observed predation is important, as this indicates that either (1) the foraging behaviour is not solely determined by the feeding state of the predator, but is also affected by prey abundance in other ways, or that (2) the behavioural observations did not allow the predators to perform their full behavioural repertoire. Identifying these shortcomings allow us to design behavioural experiments that are more likely to capture all key processes, including satiation, that determine prey consumption rates.

Prey abundance and other state variables

When the consumption rates are not adequately predicted based on satiation driven behaviour alone, the components of foraging behaviour should be assessed as

a function of satiation as well as prey density (or a related factor). If models enriched with the extra predator state variable (prey density) fail to predict as well, there is a need to include other predator state variables, like time spent in a local prey environment (patch), the buildup of nutrient deficiencies or the accumulation of toxic (prey related) substances.

Spatial scale

When nonrandom search (e.g. due to olfactory information) can be important at scales larger than e.g. leaf disks, these scales should be included in the range of experiments.

Flexible behaviour

The nonrandom search that result from responses of predatory arthropods to prey related cues need not be fixed, but can be modified by conditioning or associative learning (Takabayashi et al. 1994, Drukker et al. 2000a, b). When assessing components of foraging behaviour in relation to satiation or other variables, it is critically important that the predators have an adaptation period in the new prey environment prior to the observations. During that adaptation period they may gather information about their new environment, and by conditioning and associative learning they may develop a response that is ultimately constant given their state. Only at the right spatial and temporal scale the predators will perform the full behavioural repertoire that determines the functional and numerical responses to their prey.

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Appendix. 1. Simple, deterministic models for satiation-driven predation

Neglecting the stochastic nature of the predation process, the change in satiation can be described by the differential equation:

$$\frac{\partial s}{\partial t} = xg(s)w(s) - as \tag{A1}$$

where s is the relative level of satiation, x the current prey density (# cm^{-2}), g(s) the prey capture function (cm^2 day^{-1}), w(s) the amount of food ingested per prey relative to the gut capacity, and a the rate constant of gut clearing (day^{-1}). Equation A1 equals zero when the rate of ingestion balances the rate of gut clearing (Eq. 9), from which the steady state value for s ($=\hat{s}$) can be solved. With g(s) described by Eq. 2, explicit solutions are derived for two different assumptions for w(s).

Small prey content

If the amount of food ingested per prey is limited by the food content of the prey only:

$$w(s) = w_p \tag{A2}$$

balance equation (Eq. 9) can be solved explicitly for $\hat{s}$. In case $z \neq 0$, the solution is quadratic with one positive but complicated root. In case $z = 0$, the prey capture function is linear:

$$g(s) = (c - s)b \tag{A3}$$

and Eq. 9 is linear as well, with the solution:

$$\hat{s} = \frac{cw_p bx}{a + w_p bx} \tag{A4}$$

The resulting functional response (Eq. 10a) is given by

$$F(x) = xg(\hat{s}(x)) = \frac{cax}{a + w_p bx} \tag{A5}$$

This equation is similar to Holling's (1959) disk equation,

$$F(x) = \frac{a'x}{1 + T_h a'x} \tag{A6a}$$

when redefining its parameters a′ ('attack rate') and T_h ('prey handling time') as:

$$a' = \frac{1}{c} \text{ and } T_h = \frac{w_p b}{ca} \tag{A6b}$$

Large prey content

If the food content of a prey is more than a predator can ingest, the amount of food ingested per prey is limited by the predator's gut capacity:

$$w(s) = 1 - s \tag{A7}$$

The resulting balance equation (Eq. 9) is always quadratic, but its positive root is relatively simple in case the capture threshold equals full satiation ($c = 1$):

$$1 - \hat{s} = \frac{a}{2(bx - za)}\left(\sqrt{1 + 4(1+z)\frac{b}{a}x} - 1 - 2z\right) \tag{A8}$$

This results in the following functional response:

$$F(x) = \frac{a}{2(1+z)}\left(\sqrt{1 + 4(1+z)\frac{b}{a}x} - 1\right) \tag{A9}$$

More generally ($c < 1$), the functional response is described by:

$$F(x) = \frac{a}{2(1+z)}\left(\sqrt{1+2(1+c+2cz)\frac{b}{a}x + (1-c)^2\left(\frac{b}{a}x\right)^2} - 1 - (1-c)\frac{b}{a}x\right) \tag{A10}$$

Predation – oviposition relationship

Assuming steady state, the relation between predation and satiation is given by Eq. 10a:

$$F(x) = xg(\hat{s}(x)) \tag{A11}$$

With g(s) defined by Eq. 2, s can be written explicitly as:

$$\hat{s}(x) = \frac{cbx - F(x)}{zF(x) + bx} \tag{A12a}$$

which simplifies when the capture function is linear ($z = 0$) to:

$$\hat{s}(x) = c - \frac{F(x)}{bx} \tag{A12b}$$

Substituting this expression into the food allocation equation (Eq. 8a) yields a relationship between the functional and the numerical response. In the linear case ($z = 0$) the positive part of the numerical response equals:

$$R(x) = r(\hat{s}(x)) = \omega\left(c - \frac{F(x)}{bx} - \psi\right) \tag{A13}$$