The Impact of Supplementary Food on a Prey-Predator Interaction

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How additional food affects the functional and numerical response of a predator

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Abstract It is increasingly recognized that polyphagy and omnivory play a crucial role in determining ecosystem dynamics. Yet, little is known how they influence the shape of functional and numerical responses to each prey in a multi-prey environment. Holling’s time budget models are commonly used to mimic such responses, but – even as a descriptive function – they fail to predict important features by lack of realistic assumptions. For example, Holling’s time budget models predict that the plateaus of functional responses remain unaltered when there is more than one prey/food type. However, as shown in this article using a system of predatory mites (Neoseiulus cucumeris) feeding on thrips larvae (Frankliniella occidentalis) and pollen (Typha latifolia), functional response plateaus decrease given sufficient supply of alternative food, whereas numerical response plateaus are unaffected. Using a parameterised model in which prey capture behaviour is determined by the satiation level, the reduced functional response plateau was shown to be due to the fact that pollen feeding increases satiation beyond the level where the predator stops attacking prey. The unchanged plateau of the numerical response suggests that the two food sources are (linearly) substitutable.

Whereas functional responses are better represented by satiation-driven models, the tractability of higher-order population dynamic models is better served by a simple representation of functional response functions. Hence, we propose a modified version of Holling’s time budget model that provides a qualitatively description of observed functional response curves.

Keywords: omnivory, polyphagy, predation, multi-prey functional response, numerical response, alternative food, food preference
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The importance of polyphagy and omnivory for understanding ecological systems is recognised increasingly (e.g. Murdoch and Oaten, 1975; Holt, 1977, 1983; Holt and Lawton, 1994; Polis and Strong, 1996; Bonsall and Hassell, 1997; McCann et al., 1998; Holyoak and Sachdev, 1998; Mylius et al., 2001; chapter 3.3). Especially for arthropod predators the complexities that can result from polyphagy (e.g. Rosenheim et al., 1993; Fagan, 1997; Muller and Godfray, 1997; Janssen et al., 1998; Rosenheim, 2001; Snyder and Wise, 2001) and plant feeding (e.g. Lalonde et al., 1999; Eubanks and Denno, 2000; Gillespie and McGregor, 2000; chapter 3.1) are well documented.

To fully understand the effects of polyphagy and omnivory at the population level it is essential to know how the consumption on one prey is affected by the presence and consumption of other prey or food sources. A good understanding of these functional response relationships is still missing. The usual way to model the functional response of a predator to densities of multiple prey, is to assume (as in Holling’s disk equation) that the predator is time-limited, and that the time spent handling one food item goes at the expense of searching for other food items (cf. Murdoch, 1969, 1973; Hassell et al., 1976; Cock, 1978). Despite the elegant simplicity of the resulting models, and its apparently successful use in measuring prey preference (Akre and Johnson, 1979; Coulton, 1987; Sherratt and Harvey, 1993), there are at least two main reasons why this theory does usually not apply to arthropod predators.

First, detailed behavioural observations show that most arthropod predators are not limited by time, but rather by the rate at which prey can be converted into predator biomass (Sabelis, 1992). Second, many experimental studies show a reduction of the plateau level of the prey consumption when another food source is added (McMurtry and Scriven, 1966; Elbadry and Elbehawy, 1968; Chesson, 1989; Hazzard and Ferro, 1991; Wei and Walde, 1997; Zemek, 2001), whereas these time-budget models predict that the plateau level is unaffected.

The first controversy has been the reason to develop satiation-driven predation models (Holling, 1966; Sabelis, 1981, 1985, 1986; Metz and Van Batenburg, 1985ab; Van den Meiracker and Sabelis, 1999; chapter 2.4), which can be extended to include more that one food type, as outlined by Sabelis (1986, 1990) and Dicke et al. (1989). Here we investigate if these satiation-driven predation models can also resolve the second controversy. We (1) use a satiation-driven predation model that has been parameterised and tested for predatory mites feeding on thrips larvae (chapter 2.4), and extend it to include feeding on a second food source (pollen), (2) compare its predictions with experimental measurements of the plateau level of the functional response both in absence and in presence of pollen, and (3) formulate simple equations that adequately describe the results, facilitating the use of mixed-diet functional responses in higher order population-dynamical models.

Material and Methods

Predator, prey and host plant

The predatory mite, Neoseiulus cucumeris (Oudemans), originated from Bionomics Ltd. in Vancouver, BC, Canada, and has the ability to enter reproductive diapause under short-day conditions. In our laboratory the population was maintained on bean leaves infested with spider mites, and was transferred to a diet of Vicia fabae pollen a few weeks before the experiments. The mites were kept at 25 °C, 62% RH and L:D 16:8 h in
plastic arenas, with edges of wet tissue paper that served as a water source (chapter 2.2). For the experiments, gravid female predators were taken from cohorts that were initiated by collecting eggs 11 days before.

The prey, Frankliniella occidentalis (Pergande), originated from the DLO-CPRO in Wageningen, The Netherlands, and was reared for several years on potted chrysanthemum plants (Dendranthema indicum), supplemented with cattail pollen, in a 2 m³ incubator at 25 °C, 80% RH and L:D 16:8 h. The thrips larvae that served as prey were obtained from eggs that were laid c. 4 days earlier on detached cucumber leaves, placed upside down on moist cotton wool. As prey size appears to be decisive for the results of predation experiments, the larvae selected for the experiments were all 0.5 to 0.6 mm long (Van der Hoeven and Van Rijn, 1990).

Cucumber plants, Cucumis sativa L., cv. Ventura RZ™, were grown from seeds in a growth chamber at 25 °C until having 5-7 leaves. The third to fifth full-grown leaves were used as substrate in the experiments.

**Experimental set-up**

The rates of predation and oviposition were determined at three densities of thrips larvae, both with and without pollen, at 25 ± 1 °C, 62 ± 3% RH and L:D 16:8 h.

Circular leaf disks were put upside down on wet cotton wool and provided with a fixed number of thrips larvae. Three different initial prey densities (0.07, 0.4, 2.7 larvae/cm²) were obtained by varying both the number of thrips larvae and the disk size in the following combinations: 8/120, 10/25 and 12/4.5 larvae/cm². These numbers were chosen to obtain a large (40-fold) range in prey densities with prey numbers high enough to avoid the risk of prey depletion. Prey numbers were at least 3 times the number of prey killed between two observations (c. 12 hours). On some of the leaf disks a surplus of cattail pollen (Typha latifolia L., 20-40 µg/cm²) was dusted evenly over the disk with a brush. Each disk was provided with one gravid female predator. After 24 and 48 hours each predator was transferred to a new leaf disk that was provided with prey of right number and size. To further limit the variation in prey density and prey size, the disks were checked again 10-12 hours after each transfer, and all larvae that were killed or had grown beyond 0.65 mm were replaced. After each predator transfer, predator eggs and both killed and alive thrips larvae were counted and removed from the leaf disk. After incubation for 3 to 4 days at 25 °C the disks were checked again on the presence of juvenile predators, as the transparent predator eggs (that hatch after two days) are regularly missed at first observation. Because the predatory mite may have to adapt to the new environment, and may produce eggs resulting from the food consumed the day before, only data from the last 48 hours were used to estimate per capita predation and oviposition rates. The experiments were replicated c. 10 times for every prey density in the absence of pollen and c. 14 times in the presence of pollen, as more variation was observed in the latter treatment.

The effects of prey density and pollen availability on prey consumption and oviposition were tested by a 2-way analysis of variance in a 3 × 2 design.

**Satiation-driven mixed-food predation model**

The time-differential equation that describes the probability distribution of satiation levels \( p(x) \) (Metz et al., 1988; chapter 2.4) is extended with two extra terms to include feeding on the alternative food:
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\[
\frac{dp(s)}{dt} = -\frac{\partial sp(s)}{\partial s} - x_1g_1(s)p(s) + x_1g_1(s-w_1)p(s-w_1) - x_2g_2(s)p(s) + x_2g_2(s-w_2)p(s-w_2),
\]

where \( a \) represents the relative rate of gut clearing, \( x \) the density of food source \( i \), \( w \) the food content of one item of food type \( i \) relative to gut capacity, and \( g_i(s) \) is the 'prey capture function' for food type \( i \). The latter is assumed to be a declining function of satiation according to

\[
g_i(s) = \begin{cases} \frac{b_i(c_i - s)}{1 + z_i s} & s < c_i, \\ 0 & s \geq c_i, \end{cases}
\]

where \( b_i \) determines the maximum effective search rate, \( c_i \) the so-called capture threshold (the satiation level at which the prey capture rate just becomes zero), and \( z_i \) a shape parameter. When \( z_i = 0 \) the positive part of the function reduces to \( b_i(c_i - s) \), in which case prey capture declines linearly with increasing satiation up to \( c_i \). When \(-1 < z_i < 0\) the function is concave, when \( z_i > 0 \) convex.

Assuming that prey density changes at a much lower rate than the predator’s satiation, the probability distribution of satiation \( p(s) \) can now be assumed to be in a pseudo-steady state, which can be solved for every pair of \( x_i \)-values by putting equation 1 equal to zero. For the mixed-food functional response analytical limit-case approximations (Metz et al., 1988; chapter 2.4) are not available, but the steady state distribution of satiation levels (\( \hat{p}(s) \)) can be calculated numerically, as explained by Metz et al. (1988).

The mean rate of predation on food source 1 (= thrips larvae) equals the \( p \)-weighted average of the predation rates at each satiation level:

\[
F_1(x_1, x_2) = \int_0^1 x_1g_1(s)\hat{p}(s)ds.
\]

Assuming that the two food sources are substitutable, and that food is allocated to reproduction only after maintenance requirements are met, the reproduction rate at satiation level \( s \) can be written as:

\[
r(s) = \begin{cases} \omega(s-\psi) & \text{if positive}, \\ 0 & \text{otherwise}, \end{cases}
\]

where \( \omega \) is the food conversion rate, and \( \psi \) the maintenance ratio (see for definition and measurements chapter 2.4).

The mean oviposition rate in the predator population equals the \( p \)-weighted average of \( r(s) \):

\[
R(x_1, x_2) = \int_0^1 r(s)\hat{p}(s)ds.
\]

When the changes in satiation of individual predators are relatively fast compared to the assimilation rate, the individual reproductive response may simple be calculated on the basis of their mean satiation level (\( \bar{s} \)):
Table 1 Variables, functions and parameters of the satiation-driven mixed-food predation model. Parameter values for *N. cucumeris* feeding on *F. occidentalis* (*i* = 1) and cattail pollen (*i* = 2) based on chapter 2.4 or explained in the text.

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
<th>Default values</th>
<th>Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>variables and functions</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>x</em></td>
<td>prey density</td>
<td></td>
<td>cm²</td>
</tr>
<tr>
<td><em>s</em></td>
<td>satiation (gut content relative to gut capacity)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>p</em>(s)</td>
<td>probability density function of <em>s</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>g</em>(s)</td>
<td>prey capture function</td>
<td></td>
<td>cm²/day</td>
</tr>
<tr>
<td><em>F</em>(x)</td>
<td>predation rate (functional response)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>R</em>(x)</td>
<td>oviposition rate (numerical response)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>parameters</strong></td>
<td></td>
<td><em>i</em> = 1</td>
<td><em>i</em> = 2</td>
</tr>
<tr>
<td><em>A</em></td>
<td>rate of gut clearing</td>
<td>2.4</td>
<td>2.3</td>
</tr>
<tr>
<td><em>A</em></td>
<td>rate of digestion</td>
<td>2.3</td>
<td></td>
</tr>
<tr>
<td><em>b</em>₁</td>
<td>capture rate constant</td>
<td>82.3</td>
<td>143</td>
</tr>
<tr>
<td><em>c</em>₁</td>
<td>capture threshold</td>
<td>0.76</td>
<td>1</td>
</tr>
<tr>
<td><em>z</em>₁</td>
<td>shape parameters of prey/pollen capture function</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>w</em>₁</td>
<td>food ingested per capture relative to gut capacity</td>
<td>0.73</td>
<td>0.03</td>
</tr>
<tr>
<td><em>ω</em></td>
<td>conversion rate</td>
<td>5.5</td>
<td>0.35</td>
</tr>
<tr>
<td><em>y</em></td>
<td>maintenance ratio</td>
<td>0.26</td>
<td></td>
</tr>
</tbody>
</table>

\[
R(x₁, x₂) = r(\tilde{s}(x₁, x₂)) \quad \text{where} \quad \tilde{s}(x₁, x₂) = \int_0^1 \frac{1}{s} p(s) ds .
\]  

(4c)

The parameters of the reproduction function (4), as well as the capture function with thrips as prey (*i* = 1), are known (chapter 2.4) (Table 1). The pollen capture function, *g*₂(*s*), representing the rate at which predators able to find pollen, is largely unknown. Assuming random search, its maximum (*g*₂(0)) will not exceed 127 dm²/day, which is obtained as the product of walking speed (0.43 mm/s), walking activity (0.72) and width of the searching path (0.51 mm, with the size of the pollen being negligible) (chapter 2.4). The chance that when crossed by a predator a pollen grain will be detected and emptied (success ratio) is not known but will be much lower than one. From comparison with other small food items such as spider mite eggs (Sabelis, 1986; Metz et al., 1988), we can assume (1) that the capture threshold (*c*₂) will be close to one, and (2) that the capture function will be linear or concave (*z*₂ ≤ 0). More precise estimates cannot be given, and both *b*₁ and *z*₁ will therefore serve as fitting parameters. A pollen grain contains much less water than insect prey, and predatory mites fed with pollen also need to drink free water (chapter 2.2). To estimate the increase in satiation after feeding on a pollen grain (*w*₂), it is assumed that the pollen content is supplemented with water to yield a protein concentration similar to the hemolymph of insect larvae (c. 3%, e.g. Smaggh et al., 1999; Nakamatsu et al., 2001). The pollen of *Typha latifolia* has an estimated dry weight of 0.0243 µg (based on its volume of 6.9 × 10⁻⁵ cm³ and the volume-weight regression, both given by Roulston et al., 2000) of which 19.2%, or 4.66 × 10⁻³ µg, is reported to be protein (Roulston et al., 2000). Dilution of the pollen protein to the concentration found in insect hemolymph (3%) yields a total food weight per pollen grain of 4.66 × 10⁻⁷/0.03 = 0.155 µg. When taken relative to the gut capacity (5.2 µg), *w*₂ is 0.03.
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Figure 1 The functional (a) and numerical (b) response of *N. cucumeris* to the density of first stage thrips larvae in absence (open symbols, drawn lines) and presence (closed dots, dashed lines) of pollen. Symbols indicate experimental results (means, confidence intervals). Lines indicate either (a₁, b₁) results from the satiation-driven model for an effective pollen density (x₂) of 3/cm² (see text, Table 1), or (a₂, b₂) descriptions by Monod-type models (eq. 7 and 9). In the latter case the functional and numerical responses are simultaneously fitted to the data points at lower and intermediate prey densities (f₁ = 5.4/day, h_F = 0.011/cm², φ = 0.59 10⁻⁴ prey/pollen, k = 14 10⁻⁴ cm²/pollen, R_m = 4.5/day), with m (= 0.33) and h_R (= 0.005/cm²) fixed at values that are calculated as indicated in text and tables.

Table 2 Two-way analysis of variance: the effects of prey density and pollen availability on predation and oviposition rate of *N. cucumeris* on cucumber leaf disks with young thrips larvae.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Predation rate</th>
<th></th>
<th>Oviposition rate</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>MS</td>
<td>F</td>
<td>p</td>
<td>MS</td>
</tr>
<tr>
<td>prey</td>
<td>2</td>
<td>4.65</td>
<td>2.83</td>
<td>0.067</td>
<td>0.47</td>
</tr>
<tr>
<td>pollen</td>
<td>1</td>
<td>194</td>
<td>118</td>
<td><strong>0.000</strong></td>
<td>0.21</td>
</tr>
<tr>
<td>interaction</td>
<td>2</td>
<td>0.48</td>
<td>0.29</td>
<td>0.747</td>
<td>0.25</td>
</tr>
<tr>
<td>error</td>
<td>65</td>
<td>1.65</td>
<td></td>
<td></td>
<td>0.30</td>
</tr>
</tbody>
</table>
Chapter 2.5 – Functional and numerical responses

Results

Experiments

The experimental results are summarised in Fig. 1. Despite the 40-fold difference between the lowest and the highest prey density, no significant effects of prey density on predation rate could be detected (Table 2); not even when thrips larvae are the only food source (one-way analysis of variance: df = 2.28, \( F = 1.7 \), \( P = 0.20 \)), resulting in an overall mean of 5.1 ± 1.3 larvae/day. This indicates that all prey densities are in the plateau part of the functional response curve. The effect of pollen on prey consumption, however, is much more pronounced (Table 2). Pollen causes a reduction in the consumption of thrips larvae that seems to be larger at the two lower prey densities than at the highest prey density (73%, 70%, and 56% respectively), but no significant interaction was found.

The overall mean oviposition rate was 2.7 ± 0.6 eggs/day, and was not significantly affected by prey density or by pollen availability (Table 2). In the presence of pollen, a total absence of prey did not significantly affect the oviposition rate either (one-way analysis of variance: df = 1.55, \( F = 0.71 \), \( P = 0.40 \)).

Satiation-driven predation model

The predation model, parameterised according Table 1, predicts that even at the highest prey density (2 larvae/cm²) pollen can reduce the consumption of prey (Fig. 2b). A 50% reduction is already achieved at an effective pollen density of 1.6 grain/cm². Since a similar reduction was experimentally obtained with an estimated pollen density of 1200 grains/cm², it has to be assumed that one out of 800 pollen grains crossed is actually consumed (success ratio). The strong reduction of prey consumption by pollen results from the difference in capture threshold for prey and pollen. Whereas predator satiation have to drop below c. 0.76 before prey capture rates become positive, it only have to be somewhat lower than unity before pollen consumption can occur. As a consequence, pollen consumption can shift the gut content distribution partially beyond the prey capture threshold (Fig. 2a), thereby reducing the proportion of mites that may capture prey.

Making the pollen capture function more concave \((z < 0)\) appears to have similar effects as increasing the pollen density, and does not change the results qualitatively. To investigate the effect of pollen on the functional response for the full range of prey densities, the mixed food predation model had to be adjusted for the higher foraging efficiency of this predator at lower prey densities, as described in chapter 2.4. With a constant effective pollen density (1.6 grain/cm²), the model correctly predicts the experimental data in the presence of pollen (Fig. 1a). This shows that there is no reason to infer that preference is density-dependent (switching).

Note that the oviposition data at the highest thrips density are somewhat below the curve. This can very well be the result of consumption of predator eggs by thrips larvae, as has been described by Faraji (2001). The observed deviation of 0.4 eggs/day can result from killing eggs with a per capita attack rate of 0.05 cm². At the intermediate and lower thrips densities such rate will lead to 0.06 and 0.01 of eggs killed daily, which will remain undetected.
Figure 2 (a) The effect of pollen density ($x_2$) at high prey density ($x_1 = 4/cm^2$) on: (a) the satiation distribution of the predators. The dotted line indicates the prey capture function, which becomes zero at the prey capture threshold ($c_1$, indicated by the vertical line). Due to its higher capture threshold ($c_2$) pollen increases the proportion of predators that are satiated beyond the prey capture threshold, and that will thus not feed on prey. (b) The resulting mean pollen ($F_2$) and prey ($F_1$) consumption rates. (c) The resulting mean oviposition rates ($R$) (The thin horizontal line, $R_1$, indicates level in absence of pollen feeding).
Simple descriptions of mixed-food functional and numerical responses

To obtain a more simple and explicit function describing the mixed-food functional and numerical response, it is instructive to start with Holling's disk equation that is extended to include a second prey (Murdoch, 1969; Hassell, 1978):

\[ F_i(x_1, x_2) = \frac{a_i x_1}{1 + T_1 a'_i x_1 + T_2 a'_2 x_2}, \quad (5a) \]

where \( x_1 \) is again the density of prey \( i \), \( a'_i \) is the searching or attack rate with respect to prey \( i \), and \( T_i \) the handling time of each prey item of type \( i \).

This can also be written as a Monod or Michaelis-Menten equation:

\[ F_i(x_1, x_2) = f_i \frac{x_1}{h_F + x_1 + \phi x_2}, \quad (5b) \]

by defining \( f_i = \frac{1}{T_1} \) (plateau feeding rate), \( h_F = \frac{1}{T_1 a'_i} \) (half-saturation density), and \( \phi = \frac{T_2 a'_2}{T_1 a'_1} \) (value of additional food relative to primary food).

In this basic form, the model predicts that a high prey densities the prey consumption rate approaches the same plateau level in absence and in presence of an alternative food source. The experiments and the satiation-driven model, however showed a plateau level that is reduced in presence of the alternative food. The apparent greater impact of the alternative food at higher prey densities can be mimicked by assuming that the relative importance of alternative food (\( \phi \)) increases (linearly) with prey density:

\[ \phi(x_1) = \phi_0 + k x_1, \quad (6) \]

which results in the following model for prey consumption:

\[ F_i(x_1, x_2) = f_i \frac{x_1}{h_F + x_1 + \phi_0 x_2 + k x_1 x_2}. \quad (7) \]

The last term in the denominator can also be interpreted as the interaction between the two food source densities, with a strength defined by parameter \( k \). Similar to the satiation-driven model (Fig. 2b), this functional response model predicts a plateau level that asymptotically decreases to zero with increasing density of the alternative food, since

\[ \lim_{x_i \to x} F_i(x_1, x_2) = \frac{f_i}{1 + k x_2}. \]

As this model fits reasonably well to the results of this study (Fig. 1a), as well as to that other studies (Wei and Walde, 1997; Zemek, 2001), it may serve as an approximation that can be applied in population-dynamical modelling.

Since the two food sources give rise to the same maximum oviposition rate (separate as well as in combination), the total food availability may well be approximated by the sum of the two food densities, with \( \phi \) representing the weighing factor of the alternative food relative to that of the prey. The mean satiation level as function of prey density that is predicted by the satiation-driven model can well be described by a Monod function (data not shown), resulting in:
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\[ \bar{s}(x_1, x_2) = s_m \frac{x_1 + \phi x_2}{h_R + x_1 + \phi x_2}, \]  

(8)

where \( s_m \) is the maximum satiation level, which is close to the capture threshold \( c \), and \( h_R \) the half saturation density. Combining this with equations (4ac), the mean oviposition rate is described by:

\[ R(x_1, x_2) = \begin{cases} R_m \left( \frac{x_1 + \phi x_2}{h_R + x_1 + \phi x_2} - m \right) & \text{if positive,} \\ 0 & \text{otherwise} \end{cases}, \]  

(9)

where \( m = \psi / s_m \) represents the maintenance costs, and \( R_m = \omega s_m \) defines the maximum oviposition rate in absence of maintenance costs.

With parameters \( m \) and \( h_R \) fixed at values estimated from the adjusted satiation-driven model (chapter 2.4, Table 1), this function is able to fit the experimental results adequately (Fig. 1b2). Since the functions for the functional and numerical responses share one parameter (\( \phi \)), they have been fitted simultaneously. Oviposition data at the highest prey density have been excluded for reasons explained before.

Discussion

Functional response

Numerous predation studies have shown that providing an additional food source results in a reduction of the consumption on the original prey (e.g. Sherratt and Harvey, 1993; Lucas et al., 1997; Eubanks and Denno, 2000). As far as they assessed the plateau of the functional response (McMurtry and Scriven, 1966; Elbadry and Elbenawy, 1968; Chesson, 1989; Hazzard and Ferro, 1991; Wei and Walde, 1997; Zemek, 2001), they all showed that providing additional food even reduces the plateau level of the functional response to the original prey.

Our study also provides clear evidence for a decreased plateau of the functional response when thrips larvae are supplemented with pollen. Classic (time budget) functional response models cannot explain such results. Satiation-driven models, however, do provide a mechanistic explanation, and indicate under what conditions this result can be expected. When lower satiation levels are required for the predator to attack the prey than to feed on the additional food (i.e. the capture threshold for the prey is lower than that for the additional food, \( c_1 < c_2 \)), the additional food will result in satiation levels close to and above the threshold for prey capture (even at very high prey densities, Fig. 2a), resulting in a strongly reduced plateau prey consumption (Fig. 2b). This strong reduction will even occur when the \( c_2 \) is only slightly above \( c_1 \) (Fig. 3), but will rapidly disappear when \( c_2 \) is becomes lower that \( c_1 \). In other words, when the capture threshold for the additional prey is clearly lower than that for the first prey \( (c_1 > c_2) \) the model predicts no decreased plateau predation in the presence of the additional prey. This sensitivity of the model for relative differences in capture thresholds for the different prey may provide a good experimental test for this theory.
Figure 3 The effect of the relative positions of the two prey capture thresholds on the plateau prey consumption levels (thick lines for prey 1, thin lines for prey 2). When the second prey has small food content, as for pollen \((w_2 = 0.03, \text{black lines})\), the transitions are steeper than when it has food content similar to the first prey \((w_2 = 0.77, \text{grey lines})\). In this graph \(c_1 = 0.76, x_1 = 4/cm^2\) and \(x_2 = 100/cm^2\).

Numerical response

When a diet is supplemented with food of a different kind (as in our study thrips and pollen) the general expectation is that the reproduction or developmental rate will increase, even when the total food density will be kept constant; the food sources are assumed to be complementary (Tilman, 1982). These benefits of a mixed diet are well documented for arthropod predators, both when prey is supplemented with other prey (Dean and Schuster, 1995; Toft and Wise, 1999ab; Hagele and Rowell-Rahier, 1999; Evans et al., 1999; Bilde and Toft, 2001), with nectar or honeydew (Zhimo and McMurtry, 1990; Limburg and Rosenheim, 2001; chapter 2.3), or with pollen (McMurtry and Scriven, 1966; Boukary et al., 1998; Perdikis and Lykourressis, 2000). In our study, however, the total reproduction does not increase when adding pollen to a diet of thrips larvae, whereas pollen-fed predators showed similar oviposition rates than thrips-fed predators (Fig. 1b). This indicates that these food sources (despite their difference in nature) should be regarded as (linearly) substitutable (Tilman, 1980; Abrams, 1987). When this is the case the numerical response can simply be described by equation 5. In case of complementary food sources, an interaction term \((px_1x_2)\) could be added to the numerator, representing the benefit of a mixed diet.

Implications for ecological theory

The understanding that predation is often more limited by gut capacity than by prey handling time may have important implications for the role of polyphagy in ecology. Here we will discuss the possible consequences for three fields of ecological theory: (1) prey preference, (2) optimal foraging theory, and (3) population dynamics.
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(1) Preference for one food type over another is traditionally defined as the ratio between the respective attack rates, \( a_2^*/a_1^* \), as defined for the mixed-prey disk equation (5a) (Cock, 1978), and switching as a positive relationship of this preference with the ratio of the respective food densities, \( x_2/x_1 \) (Murdoch, 1969; Hassell, 1978). When this preference index would have been estimated by fitting the functional response with the disk equation (5a) we would have concluded that preference for pollen over thrips would increase with thrips density (eq. 6) (as in Chesson, 1989; Heong et al., 1991), indicating negative switching behaviour (to be expected for non-substitutable resources; Abrams, 1987). The satiation-driven predation model, however, can explain the observed shift in predation rates without assuming any change in behaviour. This points out the danger of drawing conclusions from fitting the disk equation in situations where the basic assumption of time limitation is not met.

(2) Optimal Foraging Theory (OFT) has traditionally been formulated in terms of time budgets as well (Charnov, 1976; Abrams, 1987; chapter 3.3). When ignoring qualitative differences between prey types, the assumption of time limitation logically results in a prey profitability that is defined as the ratio between food content and handling time \( (w/T) \). A satiation-driven predator however will maximise its reproduction by maximising its satiation level. Model sensitivity analysis for high prey densities (chapter 2.4, Fig. 5) shows that of all parameters the capture threshold \( c \) has the largest impact on satiation, followed by food content \( w \). Prey profitability under satiation limitation will therefore first-of-all be related to the prey-related capture threshold, and will consequently rank differently than prey profitability under time limitation. In our example the oviposition rate shows an initial decrease with increasing pollen density (Fig. 2c), which means that OFT (maximising oviposition rate) would predicts that the predator should ignore pollen as long as its density is below a critical level. This initial decrease occurs only at relatively high prey densities (in our example \( x_1 > 2 \)) and when (as in our example) the two food sources are very different in both content \( (w) \) and capture threshold \( (c) \). These predictions are principally different from the classic OFT where the switching point is dependent on the density of the preferred prey only. In our example, the predicted benefits of disregarding pollen at low densities are probably too marginal to expect detectable adaptations, but this might very well be different in other systems.

(3) An additional food source will affect the local population dynamics of polyphagous predators and their prey in two different ways. First, it will increase predator reproduction when prey density is low and consequently reduce equilibrium levels of the prey or drive the prey to extinction (Holt, 1977; Holt and Lawton, 1994; chapter 3.1). Second, it will reduce per capita predation rates and consequently reduce stability and resilience, which may result in higher prey levels during the transient phase (Abrams et al., 1998, chapter 3.1), or even in uncontrolled growth of the prey population. Our study showed that additional food not only reduces prey consumption rates at low prey densities, but also at densities where the functional response would be at its plateau. Including this phenomenon into population dynamical models is expected to have only minor impact on the stability of the equilibrium, since an equilibrium prey densities is always below the saturating zone of the numerical response, and consequently well below the saturating zone of the functional response (Fig. 1). It may, however, seriously aggravate the fluctuations during the transient phase (Abrams et al., 1998; chapter 3.1).
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