The Impact of Supplementary Food on a Prey-Predator Interaction
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3.1

How plants benefit from providing food to predators even when it is also edible to herbivores

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**Abstract.** It is well established that plants provide alternative foods to predators of herbivorous arthropods. This provision may facilitate protection against herbivory. However, plants often cannot prevent other organisms from utilizing these foods as well. There are many examples of herbivorous arthropods that can feed on plant-provided foods such as extrafloral nectar and pollen. The question therefore arises whether individual plants still gain protection when not only the predators but also the herbivores can feed on these foods. We investigated this question using a mathematical model and experiments that assessed the impact of supplementary pollen on the dynamics of predatory mites (*Iphiseius degenerans* (Berlese)) and herbivorous thrips (*Frankliniella occidentalis* (Pergande)), two arthropods capable of using pollen for reproduction. Replicated greenhouse experiments showed that biweekly addition of pollen to one young mature leaf of a male-sterile cucumber plant increased predator population growth and greatly reduced herbivore numbers. A stage-structured predator-prey-pollen model with experimentally established parameters gave reasonably accurate predictions of population trends observed in the greenhouse experiments with and without pollen. Model analysis yielded three important results. First, herbivore (= prey) equilibria always settled to lower values in the presence of pollen. Second, mean herbivore numbers during the transient phase following predator release were not always lower under pollen supply, depending on the initial numbers of predators and prey. Third, limiting the plant area covered with pollen led to a decrease in mean herbivore numbers, provided the predators aggregate in (and thereby ‘monopolize’) pollen patches. The latter result may explain why plants provide alternative foods at specific sites.

**Keywords:** omnivory, apparent competition, intraguild predation, tri-trophic interactions, predator-prey interaction, plant-predator mutualism, indirect plant defense, alternative food, pollen, biological control, structured populations
Plants can influence the performance of natural enemies of their arthropod herbivores in a variety of ways. They may provide them with shelter, alternative foods or information-conveying chemicals. The herbivores' enemies may make good use of these plant-provided facilities and, as a result, the plants may benefit by being better protected against herbivore attack. Such mutualistic interactions are never cheater-proof (Bronstein, 1994). Once plants invest in plant-predator mutualisms, they cannot prevent other organisms from reaping the benefits, and these organisms may well include the enemies of the plant. Indeed, there are several examples of herbivorous arthropods exploiting plant-provided shelter, chemical alarms and foods (Sabelis et al., 1999).

We investigate whether a plant benefits from producing alternative food when this is eaten not only by predators, but also by herbivores. Plant pollen is the source of alternative food under consideration. Clearly, pollen has evolved primarily for its role in sexual reproduction in plants, but as a result of mate competition, it is generally produced in large quantities and only a small fraction ends up on the stamen of another flower, thereby allowing the remaining pollen to perform other functions. One such function is to serve as a food source for mutualists, and plants may well be able to manipulate the nutritive quality and edibility to pollinators as well as to predators that may serve the plant as bodyguards. Pollen can be utilized by several groups of predatory arthropods (chapter 1.2), such as heteropteran bugs (Alomar and Wiedenmann, 1996), ladybird beetles (Cottrell and Yeargan, 1998; Trilich, 1997), hoverflies (Haslett, 1989; Warrant et al., 1995), green lacewings (Sheldon and MacLeod, 1971) and predatory mites (chapter 2.2). However, there are also groups of herbivorous arthropods which use pollen to promote their survival and reproduction, such as chrysomelid and curculionid beetles (Jayanth et al., 1993; Jones et al., 1993), lycaenid and Heliconius butterflies (Wagner and delRio, 1997; Gilbert, 1972), and many thrip species (Kirk, 1997). We studied the impact of pollen on the dynamics of the western flower thrips, Frankliniella occidentalis Pergande (Insecta, Thysanoptera, Thripidae), and the predatory mite, Iphiseius degenerans (Berlese) (Acari, Mesostigmata, Phytoseiidae), on cucumber plants. The thrips have been shown to increase their reproduction when fed on pollen and leaves together (Hulshof and Vänninen, 1999), whereas the predatory mites are known to increase in numbers even on a diet of pollen alone (chapter 2.2). This predator-herbivore-plant system (Fig. 1) is therefore ideally suited to answer the question whether the production of edible pollen reduces herbivore damage to the plant by promoting the effectiveness of predators, in spite of the fact that herbivores utilize pollen as well.

There is a large body of theory showing – with some rather special exceptions (Abrams and Matsuda, 1993, 1996) – that the addition of alternative foods or prey to the predators in a predator-prey system reduces the equilibrium level of the primary prey population (‘Apparent Competition’, Holt, 1977, 1983; Abrams, 1987, 1998). Provided the alternative food suffices to achieve positive growth of the predator population, the prey population may even go extinct (Holt et al., 1994; Holt and Lawton, 1993, 1994; Bonsall and Hassell, 1997). These conclusions do not simply translate to non-equilibrium dynamics. For example, Abrams et al. (1998) showed that under a regime of predator-prey cycles the addition of another prey does not necessarily reduce the mean densities of the primary prey. At the population level, it may even seem as if the two prey species profit from each other’s presence! Clearly, for other types of population fluctuations, including transients towards equilibrium, one should be cautious in inferring that the addition of one prey has negative effects on the other via their shared predators. Since real populations never settle exactly at an equilibrium, it is essential to investigate under which dynamical regimes these indirect effects occur. Moreover, no
such analysis has yet been made of the case where the additional prey (or food) is eaten not only by the predator, but also by the primary prey.

In this article, we assess the theoretical conditions under which plants will accommodate less herbivores when providing alternative food, in spite of the fact that not only the predators but also the herbivores can utilize it. We test the underlying model against observations of the effect of alternative food on the dynamics of predatory mites and herbivorous thrips in a greenhouse. Finally, we briefly discuss how our findings provide insight in the role of food provisioning in the evolution of plant-predator mutualism.

Materials and Methods

Population experiments

The predatory mite *Iphiseius degenerans*, originally collected in Morocco in 1984, was initially reared on iceplant pollen by Dr. J.M. McMurtry (UC Riverside, CA) and, since 1991, on birch pollen in our lab in rectangular PVC arenas (25 °C, 62% RH) (chapter 2.2). The herbivore *Frankliniella occidentalis* was obtained from a culture on cucumber, started with a sample from a greenhouse in Naaldwijk, The Netherlands. As the alternative food source, we chose pollen from common cattail, *Typha latifolia* L., as it (1) is known to be a good food source for rearing the predatory mites (chapter 2.2), (2) is easy to collect in large quantities, and (3) retains good quality for several weeks under the usually humid greenhouse conditions (Y.M. van Houten, unpublished results). The pollen was collected from plants on the university campus in Amsterdam, and then dried, sieved and stored as described in chapter 2.2.

![Figure 1](https://via.placeholder.com/150)

**Figure 1** Food web diagram of the experimental system. Arrows indicate flow of material.
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The population experiments were carried out in 1997 at the Research Station for Floriculture and Glasshouse Vegetables (PBG, Naaldwijk, The Netherlands) in four greenhouse compartments (76 m² each) with cucumber plants. The compartments were separated by crop-free corridors (3.2 m width) to prevent cross-contamination, and were provided with gauzed windows to reduce immigration of insects. The cucumber crop was maintained according to current growers’ practice (PBG; Anonymous, 1996), implying that temperature was computer-controlled (min. 19 °C, max. 26 °C, mean 22 °C). Humidity was not controlled and varied mostly between 70 and 90% RH, with lower values only at the start and the end of the experiment. The main stem was trimmed beyond leaf number 19, and all side shoots were removed, except for two at the top of the main stem and the first one (or two) appearing on every side shoot. All four (to six) side shoots were allowed to grow down.

In the second week of 1997, each of the four compartments was provided with 108 cucumber plants (Cucumis sativa L., cv. Enigma). The plants, rooted in blocks of rock wool, were arranged in 12 rows. In the 2nd and the 4th week, 60 adult females of the plant-feeding thrips Frankliniella occidentalis were released in each compartment. In the 4th week four female predators (10-13 days since hatching) were introduced on every plant, which by then had 9-10 fully-grown leaves. This introduction was repeated twice in the control compartments (four females/plant in week 7 and 10) after the predator populations were found to be nearly extinct. In the two other compartments, cattail pollen (10-15 mg per plant) was introduced every other week. Preliminary experiments showed that when cattail pollen is kept for 14 days on cucumber leaf in a greenhouse and offered as a food source to the predators, it still allows 75% of the juveniles to mature, whereas adult females oviposit at half a rate compared with fresh pollen (Van Houten, unpublished data). The pollen was always introduced on one leaf of every plant according to the following schedule (always directly after population monitoring): (1) initially (week 4) on the 8th leaf from below, (2) leaf 16 in week 6, (3) 1st leaf on 1st side shoot in week 8, and (4) 2nd leaf on the other 1st side shoot in week 10. By the end of the monitoring period (week 15) the plants had on average 38 leaves, excluding the c. 7 leaves on the main stem that were removed when they died off.

The adult female thrips were monitored with two blue sticky traps (Koppert® BV) per compartment. They were initially replaced once a week, but when the numbers trapped exceeded 1000 per week the trapping period was reduced to 24 hours per week. Juvenile thrips and predator populations were estimated based on in situ observations of 8-16 representative leaves from 10 plants per compartment (one randomly selected plant per row). Initially, all leaves on a plant were checked for mites and thrips, but later, due to the increase in plant size, only one of every two or three leaves could be monitored. The leaves that had been provided with pollen were monitored always. The total population size per plant was estimated, assuming that non-sampled leaves had the same number of mites and thrips as the nearest sampled leaf (excluding the leaves with pollen). The first 6 weeks, the treatment compartments were sampled weekly, whereas the control compartments were sampled every other week. Later, because of labor constraints, both treatment and control compartments were sampled at biweekly intervals in an alternating scheme.

Since treatments were administered to compartments, each with many plants, there are two replications per treatment. To test whether treatment and control differ, an ANOVA with repeated measures was carried out. For this purpose we used leaf counts from the weeks in which both treatment and control have been monitored (week 5, 7 and 9) as well as from week 11 and 13 where we estimated the missing data from the control by interpolation. To improve normality all data were log-transformed. To correct for
deviations from the sphericity assumption, the degrees of freedom for the within-subject factors (time and interaction) are adjusted according the conservative Greenhouse-Geisser method (Looney and Stanley, 1989).

**Predator-prey model**

To pinpoint the conditions under which plants profit from pollen production we constructed a predator-prey-pollen model framed in (delay-) differential equations.

The pollen \( (A) \) is assumed to be produced at a constant rate \( (a) \), removed at a rate proportional to its density by natural decay \( (b) \), and removed due to consumption by thrips and predators \( (C) \), explained further-on:

\[
\frac{dA}{dt} = a - bA(t) - C(t).
\]  

(1)

The thrips population \( (N) \) is structured into three classes: (1) vulnerable juvenile phase (small larvae), (2) invulnerable juvenile phase (large larvae, pupae in the soil, pre-ovipositing females and eggs, as the latter are inserted in the leaves), and (3) invulnerable reproduction phase (ovipositing females). By taking the egg stage together with later developmental stages, the reproductive females are assumed to directly produce larvae rather than eggs, but only after a delay equal to the egg hatching period.

Thrips densities \( (N_i) \) with \( i \) indicating the class number) are expressed in number per \( \text{dm}^2 \), corresponding to the scale of laboratory experiments. Because the densities considered are well below the plants' carrying capacity, we assume unlimited growth of the thrips population. Abiotic mortality in the juvenile phase is taken into account as an implicit reduction factor with respect to reproduction, whereas abiotic mortality in the mature phase is represented as a constant per capita rate \( (v) \) for the adults. Together with a constant (age-independent) reproduction rate, this assumption results in a net reproduction rate of the thrips \( (i.e. \ \text{the product of reproduction and survival rates}) \) that declines exponentially with age, which is in close agreement with experimental data (chapter 2.1). By assuming a constant per capita rate of transfer from the vulnerable to the invulnerable phase \( (d_i) \), the vulnerability of the thrips also declines exponentially with age, again in agreement with experimental data (chapter 2.5). The remaining, invulnerable part of the juvenile period (class 2) is assumed to be of fixed duration \( (\tau_v) \). The reproduction rate of the thrips \( (R, \ \text{corrected for sex ratio and juvenile survival}) \) can double in the presence of sufficient pollen (Hulshof and Vänninen, 1999; chapter 2.4). By assuming satiation at higher pollen densities (type-II numerical response), this effect is described by the following Michaelis-Menten (or Monod) equation:

\[
R(A) = r \frac{L + A}{L + A + A_R},
\]

(2)

where \( r \) represents the maximum reproduction rate (at a surplus of pollen), \( L \) the value of leaf tissue as a food source for the thrips expressed in the same units as the pollen \( (A) \) (determining the rate of reproduction in the absence of pollen), whereas \( A_R \) represents the food density \( (L+A) \) at which \( R \) is half its maximum. Since even at the lowest food densities (\( i.e. \ \text{absence of pollen}) \) reproduction is already at about half its maximum, maintenance costs do not have to be modeled explicitly.

The rate at which vulnerable thrips suffer from predation is affected by their density \( (N_i) \) according to a saturating (type II) functional response model (chapter 2.4), fitted by a Michaelis-Menten equation. Predators do not have a clear preference for either pollen or prey, but they show a lower predation rate in the presence of pollen, even at the
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highest prey densities (chapter 2.4). This is modeled by adding an interaction term to the
denominator:

\[ F_\lambda (N, A) = f_\lambda \frac{N}{N + N_F + \phi A + kAN}, \]  

(3)

where \( f_\lambda \) represents the maximum predation rate, \( N_F \) the half-saturation density of
vulnerable prey, and \( \phi \) the food value of pollen relative to prey. The parameter \( k \)
('strength of food type interaction') determines the reduction of predation due to pollen
at higher prey densities, since

\[ \lim_{N \to \infty} F_\lambda (N, A) = \frac{f_\lambda}{1 + kA}. \]

The assumptions described above result in the following set of differential equations
for the structured prey population:

\[
\begin{align*}
\frac{dN_j}{dt} &= R(A(t))N_j(t) - F_\lambda (N_1(t), A(t))P_i(t) - d_jN_j(t) \\
\frac{dN_1}{dt} &= d_jN_j(t) - d_iN_i(t - \tau_\chi) \\
\frac{dN_i}{dt} &= d_iN_i(t - \tau_\chi) - \nu N_j(t)
\end{align*}
\]

(4)

As in the thrips model, the predator population \( (P) \) is structured into three classes:
(1) non-feeding juvenile phase (eggs and larvae), (2) feeding juvenile phase (nymphs and
pre-ovipositing females), (3) feeding and reproductive phase (ovipositing females).
Mortality and development is treated similarly as in the thrips model, with a constant rate
of transition from class 1 to class 2 \( (e) \), a fixed developmental delay for juveniles in class
2 \( (\tau_\chi) \), and an age-independent rate of decline in net reproduction \( (\mu) \) (chapter 2.2). The
predator rate of reproduction \( (G, \text{corrected for sex ratio and juvenile survival}) \) is directly
affected by prey and pollen density according a Michaelis-Menten function with
substitutional food sources (chapter 2.4):

\[
G(N_1, A) = \begin{cases} 
G \left( \frac{N_1 + \phi A}{N_1 + \phi A + N_G} - m \right) & \text{if positive} \\
0 & \text{otherwise,}
\end{cases}
\]

(5)

where \( \phi \) again represents the food value of pollen relative to prey, \( N_G \) the half-saturation
density of vulnerable prey, \( m \) the maintenance costs (relative to the total of maintenance
and reproduction), and \( g \) the maximum rate of reproduction (in the absence of
maintenance costs).

Adult predator mortality increases at very low food densities (chapter 2.3), and is
modeled by the inverse of a Michaelis-Menten function:

\[
\mu(N_1, A) = \mu_0 \frac{N_1 + \phi A + N_\mu}{N_1 + \phi A}, \text{ with } \mu_0(N_1, A) \leq \mu_m.
\]

(6)
where \( \mu_0 \) and \( \mu_m \) are the minimum and maximum mortality rate respectively, and \( N_u (<< N_v) \) is the prey density at which the inverse function (i.e. mean reproductive period) is half its maximum.

These assumptions result in the following set of differential equations for the structured predator population:

\[
\begin{align*}
\frac{dP_1}{dt} &= G(N_1(t), A(t))P_3(t) - eP_1(t) \\
\frac{dP_2}{dt} &= eP_1(t) - eP_1(t - \tau_p) \\
\frac{dP_3}{dt} &= eP_1(t - \tau_p) - \mu(N_1(t), A(t))P_3(t)
\end{align*}
\]

(7)

In the equations for pollen \((A)\) and thrips \((N)\), the juvenile predators are assumed to consume only a fraction \(j\) of what the adults consume (Cloutier and Johnson, 1992), so that the effective number of predators consuming either pollen or thrips is defined as

\[
P_c = jP_2 + P_1.
\]

(8)

Similarly, the effective number of thrips consuming pollen is defined as

\[
N_c = l_1N_1 + l_2N_2 + N_3,
\]

(9)

where \( l_i \) is the consumption rate of juvenile phase \( i \) relative to that of the adults.

The pollen consumption function is assumed to be symmetrical with the predation function \( F_N \):

\[
F_A(N_1, A) = \phi_A \frac{\phi_A}{N_1 + N_F + \phi_A + kAN_1},
\]

(10)

where \( \phi_A \) represents the maximum rate of pollen consumption.

The few experiments which have been carried out on pollen feeding (Kirk, 1987; Flechtmann and McMurtry, 1992) allow us to assume that the adults of both predator and prey feed at similar rates, so that the total rate of pollen consumption \((C)\) is given by:

\[
C = F_A(0, A)N_C + F_A(N_1, A)P_C.
\]

(11)

All calculations were done for the system-specific parameter values listed in Table 1.

So far we have assumed well-mixed populations of pollen, prey and predators. In our greenhouse experiments, however, pollen was only available on a restricted part of the plant. To model local pollen availability, the interaction space was divided into an area with pollen and one without. The proportion of the leaf surface area with pollen was assumed to be constant \((\alpha)\) throughout the interaction period. The proportions of the thrips and predator population within the area with pollen (respectively \( \beta \) and \( \gamma \)) were assumed to be flexibly determined by the individual’s adaptive choice between foraging in the area with pollen or in the area without. To make that choice, the predators must respond to food (pollen plus prey) density only, whereas the thrips have to balance food (leaf and pollen) density against predation risk. We assume that predators and prey cannot hip-hop to whichever of the two areas is best at a given moment. As thrips and their predators move on a two-dimensional plant surface, they can only assess the quality of the environment at close range. Therefore, they are thought to move randomly and, when their direct environment is profitable, prolong the time spent there.
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Table 1 Default parameter values used in pollen-herbivore-predator model.

<table>
<thead>
<tr>
<th>Parameter Description</th>
<th>Value</th>
<th>Unit</th>
<th>Note</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Pollen dynamics:</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\alpha$ proportion of leaves with pollen</td>
<td>0.1</td>
<td>(ratio)</td>
<td>2</td>
</tr>
<tr>
<td>$a$ pollen supply rate</td>
<td>$0.1\times10^4$ pollen dm$^{-2}$ day$^{-1}$ or $5\times10^4$ pollen-plant$^{-1}$ day$^{-1}$</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>$b$ instantaneous loss rate</td>
<td>0.21</td>
<td>day$^{-1}$</td>
<td>4</td>
</tr>
<tr>
<td>$f_s$ maximum rate of pollen consumption by thrips and predators</td>
<td>$0.07\times10^4$ pollen-adult$^{-1}$ day$^{-1}$</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td><strong>Prey (F. occidentalis) biology:</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$d_f$ developmental rate vulnerable prey phase (young larvae)</td>
<td>$1/3$</td>
<td>day$^{-1}$</td>
<td>6</td>
</tr>
<tr>
<td>$\tau_s$ developmental time invulnerable prey phase (eggs, older larvae, pupae, pre-ovipositing females)</td>
<td>15</td>
<td>days</td>
<td>7</td>
</tr>
<tr>
<td>$r$ max. rate of net reproduction, at surplus of pollen</td>
<td>4.0</td>
<td>offspring-adult$^{-1}$ day$^{-1}$</td>
<td>7</td>
</tr>
<tr>
<td>$A_h$ food (leaf + pollen) density at which its effect on prey reproduction (R) is half its maximum</td>
<td>$0.3\times10^4$ pollen dm$^{-2}$</td>
<td>8</td>
<td></td>
</tr>
<tr>
<td>$L$ food value of leaf tissue in terms of pollen density</td>
<td>$0.3\times10^4$ pollen dm$^{-2}$</td>
<td>9</td>
<td></td>
</tr>
<tr>
<td>$r_c$ instantaneous decline in adult net reproduction rate</td>
<td>0.11</td>
<td>day$^{-1}$</td>
<td>7</td>
</tr>
<tr>
<td><strong>Functional responses:</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$f_N$ maximum rate of thrips predation</td>
<td>4.0</td>
<td>prey-adult$^{-1}$ day$^{-1}$</td>
<td>10</td>
</tr>
<tr>
<td>$N_p$ prey density at which predation is half it maximum</td>
<td>1.5</td>
<td>prey dm$^{-2}$</td>
<td>11</td>
</tr>
<tr>
<td>$k$ weight of interaction between prey and pollen density, responsible for the reduction of consumption on either pollen or prey</td>
<td>0.11</td>
<td>dm$^{-2}$/10$^4$ pollen</td>
<td>12</td>
</tr>
<tr>
<td>$\phi$ value of pollen relative to prey in terms of predation, predator reproduction and survival</td>
<td>0.34</td>
<td>prey$/10^4$ pollen</td>
<td>11</td>
</tr>
<tr>
<td>$j$ consumption rate of juvenile predators relative to adult predators</td>
<td>0.25</td>
<td>(ratio)</td>
<td>13</td>
</tr>
<tr>
<td>$i_{1,2}$ (pollen) consumption rate of juvenile thrips stages (1 and 2) relative to adults</td>
<td>0.2</td>
<td>(ratio)</td>
<td>14</td>
</tr>
<tr>
<td>$v$ developmental rate non-predatory phase (eggs and larvae)</td>
<td>1.37</td>
<td>day$^{-1}$</td>
<td>15</td>
</tr>
<tr>
<td>$\tau_p$ developmental time predatory phase (nymphs)</td>
<td>6.3</td>
<td>days</td>
<td>15</td>
</tr>
<tr>
<td>$g$ max. rate of net reproduction (in absence of maintenance costs)</td>
<td>1.5</td>
<td>offspring-adult$^{-1}$ day$^{-1}$</td>
<td>16</td>
</tr>
<tr>
<td>$m$ maintenance costs (relative to the total of maintenance and reproduction)</td>
<td>0.2</td>
<td>(ratio)</td>
<td>17</td>
</tr>
<tr>
<td>$N_{ij}$ prey density at which net reproduction is half its maximum (in absence of maintenance costs)</td>
<td>1.0</td>
<td>prey dm$^{-2}$</td>
<td>18</td>
</tr>
<tr>
<td>$\mu_0$ minimum decline in adult net reproduction rate</td>
<td>0.05</td>
<td>day$^{-1}$</td>
<td>16</td>
</tr>
<tr>
<td>$\mu_m$ maximum decline in adult net reproduction rate</td>
<td>0.2</td>
<td>day$^{-1}$</td>
<td>19</td>
</tr>
<tr>
<td>$N_{ad}$ prey density at which adult mortality is half its maximum</td>
<td>0.08</td>
<td>prey dm$^{-2}$</td>
<td>20</td>
</tr>
</tbody>
</table>

1 Data for *N. cucumeris* were used when not available for *I. degenerans*. Rates measured at 25 °C were multiplied by 0.8 to be valid for 22 °C (using 11 °C as threshold; chapter 2.1);
2 See Fig. 3b;
3 10-15 mg cattail pollen/14 days; 5 x 10$^4$ pollen/mg;
4 After 14 days pollen quality as predator food source decreases with 50% (Van Houten, unpublished data), which according to $G(0,4)$ corresponds with a decrease in pollen density with 95% in 14 days;
Assuming a linear relationship between food density and residence time (see Appendix B) the proportion of predators in the area with pollen is described by:

\[ \gamma = \frac{\beta N_1 + \phi A}{N_1 + \phi A} \]  

(12)

Assuming that residence time is linearly related to food density as well as survival probability (see Appendix B), the proportion of herbivores in the area with pollen can be described by:

\[ \beta = \left[ 1 + \frac{(1-\alpha)L}{\alpha L + A} \cdot e^{-\lambda t} \right]^{-1}, \text{ with} \]

(13a)

\[ \Delta = \frac{1-\gamma}{1-\alpha} q(0) - \frac{\gamma}{\alpha} q(A') \]

being the difference between the two areas in predation risk, which in turn results from a (usually) higher relative predator abundance and a lower per capita predation rate in the area with pollen. Here, \(q(A')\) is the per-predator, lifetime risk to the herbivore of being eaten given a local pollen density \(A'\). At low prey densities this can be approximated by:

\[ q(A') = \lim_{N_i \to 0} \frac{F_N}{N_1} \frac{1}{d_i} = \frac{f_N}{Nf + \phi A'} \]  

(13b)

The division in two subspaces necessitates modifications (indicated by arrows) of the following elements of the population-dynamical model (defined by equations 1, 4 and 7):

(1) \(C\) (consumption of pollen),

\[ F_A(0, A)N_C + F_A(N_1, A)P_C \rightarrow F_A \left( 0, \frac{A}{\alpha} \right) \beta N_C + F_A \left( \frac{\beta}{\alpha} N_1, \frac{A}{\alpha} \right) \rho P_C \]
(2) $R$ (thrips reproduction).

$$R(A) \rightarrow \beta R(A) + (1 - \beta)R(0).$$

(3) $F$, $G$ and $\mu$ (predation, predator reproduction and mortality), here indicated by $U$,

$$U(N_1, A) \rightarrow \gamma U\left(\frac{\beta}{\alpha} N_1, \frac{A}{\alpha}\right) + (1 - \gamma) U\left(\frac{1 - \beta}{1 - \alpha} N_1, 0\right).$$

The model equilibria have been studied with CONTENT, a software package for numerical bifurcation analysis (Kuznetsov et al., 1996). The transient dynamics have been studied by (fixed-time step) simulations ran in Mathcad 2000, initializing the herbivore population by assuming preceding exponential growth ($r_m = 0.13$/day) at a stable age distribution, and initializing the predator population by assuming instant introduction of adults only.

**Results**

**Population experiments**

In pollen-treated compartments the predators increased in numbers immediately after their release whereas in the control compartments their numbers declined to virtually zero within a few weeks. The second predator introduction in the control compartments (in week 7, Fig. 2a) was more successful, since by then the prey density had increased sufficiently to allow the predator population to increase. Since this increase was exponential with a growth rate equal to 0.14/day, the predator number in the control compartment soon approached the level in the pollen-treated compartments where the predator population stabilized, probably due to competition for food (thrips and pollen). Thus, while at the last sampling date the number of predators did not differ between treatments, the pollen introductions resulted in significantly higher numbers of predators during the first 8 weeks (Table 2), which was due to a fast initial increase of predators when thrips density was still low. The initial difference in population growth partly resulted from a higher predator recruitment under the pollen treatment, as is evident from the sharp rise to a 3:1 juvenile:adult ratio in week 5, compared to the low 1:5 level in the controls. Later on, the juvenile:adult ratios converged to 1:1 in both treatment and control.

In the control compartments the thrips population increased more or less exponentially during the first 8 weeks with a growth rate (0.108-0.122/day for the larvae and 0.134-0.140 day$^{-1}$ for the adult females) close to the intrinsic rate of population increase at 22 °C (0.13/day, chapter 2.1). The population growth rate of thrips larvae in the pollen-treated compartments was initially only slightly lower than in the control compartments (0.055-0.091/day), but became much lower after 5 weeks (0.007-0.022/day). This yielded significant differences in mean population levels (Table 2) and in the course of population change (i.e. interaction with time, Table 2) between treatment and control.
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Figure 2 Population dynamics of predatory mites (all mobile stages) and western flower thrips (larvae and adult females) in presence and absence of cattail pollen on cucumber plants. Experimental results are indicated by symbols (closed symbols for treatment and open symbols for control). Simulation results are indicated by lines (drawn lines for treatment and dotted lines for control). As in the experiments, simulations concern numbers per plant. Whenever rates are density-dependent, densities result from dividing numbers by plant surface, which itself is an increasing function of time, approximated by the fitted logistic function: $S(t) = 108\left[1+\exp(-0.06\cdot(t-10))\right]^{-1}$ (dm$^2$, t in days since predator release). Adult thrips densities were converted into numbers trapped per week (lower panel) by multiplying with 18 dm$^2$/week, based on the fit at higher densities. The proportion of the area with pollen, $\alpha$, is fixed at 0.1. Initial numbers of thrips: 2 per plant (all stages according stable stage distribution), and adult predators: 6 per plant (representing males and females, equivalent to the 4 females that have been released in week 4). Predator introductions are repeated in the control experiments in week 7 and 10.
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Table 2 Summary of ANOVA’s of effects of pollen supply with repeated measures of the (log-transformed) population size of thrips larvae and predatory mites, and of the (log-transformed) weekly trap catches of adult female thrips. P-values for time and interaction effects based on df’s that are adjusted (with the given epsilon) for deviations from sphericity (Greenhouse-Geisser method).

<table>
<thead>
<tr>
<th>Factor</th>
<th>Predators</th>
<th>Thrips larvae</th>
<th>Thrips adults</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>df</td>
<td>F</td>
<td>df</td>
</tr>
<tr>
<td>Treatment</td>
<td>1,2</td>
<td>133</td>
<td>0.007</td>
</tr>
<tr>
<td>Time</td>
<td>4,8</td>
<td>24.3</td>
<td>0.038</td>
</tr>
<tr>
<td>Treatment × Time</td>
<td>4,8</td>
<td>9.8</td>
<td>0.087</td>
</tr>
</tbody>
</table>

$\epsilon = 0.25$ $\epsilon = 0.3$ $\epsilon = 0.21$

The populations of adult female thrips also showed initially equal growth rates in treatment and control, but started to deviate from week 11 onwards, nearly 3 weeks later than for the larvae, a delay close to the developmental time at 22 °C. Including all 10 trapping periods, the mean population levels and especially the population changes were significantly different between treatment and control (Table 2). The pollen treatment ultimately resulted in a 20-fold reduction of the number of thrips larvae (in week 11-12) and the number of adult females (in week 15).

By the end of the experiment, these differences in thrips numbers clearly resulted in different damage levels. In the pollen-treated compartments the leaves were virtually free of thrips damage, whereas in the control compartments at least 25% of the leaf surface was damaged by thrips, which is expected to result in a similar reduction in photosynthetic capacity (Childers, 1997). Moreover, the number of fruits distorted due to feeding by thrips varied from less than 20% for the treated to nearly 100% for the control compartments. By the end of the experiment (week 17) the cumulative herbivore density in the control compartments was c. 2100 thrips-days/leaf, which exceeded the threshold level of 1900 thrips-days/leaf (9.4 thrips-days/cm²), reported to reduce plant growth and fruit yield significantly (Welter et al., 1990). In the pollen-treated compartments the thrips were kept well below this level (110 thrips-days/leaf).

In summary, the presence of pollen significantly increased the effectiveness of the predatory mites in controlling the thrips population, despite the fact that both thrips and predators can utilize pollen as a food source. Note that the pollen treatment did not even increase the thrips population growth when predator density was still low. One clue as to why pollen introductions promote the predators and not the thrips is hidden in their vertical distribution within the plant (Fig. 3a). It appeared that the leaves with pollen harbored much of the population of predatory mites (> 90% in the first few weeks, later declining to 40%; Fig. 3b). Individual leaves continued to arrest predators for at least 5 weeks after pollen supply. The thrips larvae, on the other hand, did not really concentrate on the pollen-treated leaves (0-20% on pollen-treated leaves, which represented c. 10% of all leaves; Fig. 3). The thrips were always most abundant in the top of the plant, and the proportion on pollen-treated leaves became significant only when top leaves were provided with pollen (from week 9 onwards). As a consequence, the predators profit more from the local pollen supply than the thrips, while they apparently still visit thrips-infested leaves frequently enough to exert control.
Figure 3 Distribution of herbivores and predators over leaves with and without pollen. (a) Snapshot (at week 7) of the vertical distribution of predatory mites and western flower thrips larvae in cucumber plants with pollen on leaves 8 and 14. (b) Change in proportion of thrips and predator population present on leaves with pollen. Squares and diamonds indicate results from two replicate experiments and solid lines indicate model results: black symbols and thick line for the herbivores ($\beta$), grey symbols and thin line for the predators ($\gamma$). Crosses indicate the actual proportion of leaves that have been supplied with pollen less than 5 weeks ago and horizontal dashed line represent their mean value used in the model ($\alpha = 0.1$).

Predator-prey model: validation and predictions

Model validation
To test against the experimental observations, simulations were carried out with our model extended to include plant growth during the experimental period. Virtually all parameters are based on independent measurements in the laboratory or a-priori knowledge of experimental conditions ($5 \times 10^4$ pollen grains per plant per day, c. 10% of...
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The leaves supplied with pollen, 22 °C). The only exceptions are the two parameters determining dependence of adult and juvenile predator survival on food density ($N_a$ and partly $N_c$). These parameters are hard to measure at sufficiently low prey densities. Hence, they were fitted by a least-squares method such that the simulations correctly mimicked the initial decline (week 5 to 9) in the predator population observed in the absence of pollen. These curve-fitted parameters have very little impact on the dynamics later in the season, as well as in the presence of pollen, because juvenile and adult mortality become less dependent on prey density whenever food (prey and/or pollen) density is high.

With these modifications, the simulated dynamics corresponded well with the observed dynamics of predator and prey (Fig. 2). Whereas in the population experiments pollen supply was ended after 8 weeks, in the model the pollen supply rate is kept constant, which explains the higher final predator population. For the thrips, the model simulations gave an accurate description of the differences between treatment and control. However, the number of adult thrips on the sticky traps showed a faster increase than predicted by the model, which indicates a density-dependent trap chance, e.g. due to an increased flight activity at higher thrips densities.

For the predators, also the simulated distribution over leaves with and without pollen agreed fairly well with the observations (Fig. 3b). Initially, when thrips density is low, the majority of predators stay on leaves with pollen but when thrips density increases, the proportion of predators on leaves with pollen drops from > 90% to c. 40%. For the thrips, however, the model predicts that the thrips should completely avoid leaves with pollen (because of the high numbers of predator there), whereas the observations show that some of the thrips do occur on leaves with pollen (4-20%). There may be two causes for these differences between model predictions and observations. First, from week 9 onwards pollen was supplied on the now full-grown top leaves of the plant, which are also the preferred leaves for the thrips. This may have increased the coincidence between thrips and pollen. Second, the observations refer to larvae of both first and second stages. This is important because first stages stay near their birth site, and mothers avoid ovipositing near predators (P.C.J. van Rijn, pers. obs.), whereas second stage larvae may well move to a leaf with pollen as soon as they are big enough to be invulnerable for the predators. In the model, however, all stages were assumed to have the same distribution over leaves with and without pollen.

The greenhouse experiments suggest that the addition of pollen, although both predator and prey can utilize it, directly promotes population growth of the predatory mites and indirectly (via the predator) stops the growth of the herbivorous thrips population. These effects are indeed borne out from analyzing the pollen-prey-predator model, as we will show first for the equilibrium state and then for the case of transient dynamics.

**Equilibrium state**

Since our homogeneous model is of the Lotka-Volterra type, the prey equilibrium (see Appendix) is not affected by prey-related traits, but is determined by the predators’ numerical response (Holt, 1977; Oksanen et al., 1981). Feeding on pollen promotes predator reproduction and therefore decreases the herbivore equilibrium; even down to zero given a high enough rate of pollen supply (Fig. 4a). Although the presence of pollen also decreases the rate of predation on thrips and increases herbivore reproduction, these effects do not affect the herbivore equilibrium. So, feeding of the herbivore on the same food source as the predator does not alter the apparent competition principle.
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Figure 4 Effect of the pollen supply rate, $a$, on equilibrium and transient dynamics of pollen-herbivore-predator model. Model equilibria in (a) homogeneous environment ($\alpha = 1$) and (c$_1$,c$_2$) split environment (proportion supplied with pollen, $\alpha = 0.1$). In the latter case both the distributions (c$_1$) and the total population densities (c$_2$) are presented. Dashed lines indicate unstable equilibria. Mean herbivore population during first 100 days after predator release in (b) homogeneous environment ($\alpha = 1$) and (d) split environment ($\alpha = 0.1$), for two initial herbivore densities, $N(0)$: $0.03$/dm$^2$ and $0.3$/dm$^2$. Initial predator density is $0.1$ adults/dm$^2$. This predator density and the lowest herbivore density correspond with those in the experiments, assuming a plant size of $c. 60$ dm$^2$. 

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Figure 5 The effects of concentrating pollen on part of the plant surface on equilibrium densities of pollen, herbivores and predators (a, c) and mean herbivore density during first 100 days after predator release (b, d) according pollen-herbivore-predator model, for two pollen supply rates: $a = 0.1$ (default) (a, b) and $a = 0.3 \times 10^4$ grains dm$^{-2}$day$^{-1}$ (c, d). In the equilibrium cases both the distributions ($a_1$, $c_1$) and the total population densities ($a_2$, $c_2$) are presented. The dashed vertical line indicates the parameter value ($\alpha = 0.98$) at which the equilibrium herbivore density becomes zero. In (b) and (d) the initial predator density is 0.1 adults/dm$^2$. This predator density and the lowest herbivore density ($N(0) = 0.03$ thrips/dm$^2$) correspond with those in the experiments, assuming a plant size of $c. 60$ dm$^2$. 

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At intermediate supply levels ($a = 0.1$, Fig. 4ac) concentrating the pollen in a small part of the environment will further reduce the herbivore equilibrium (Fig. 5a). Since the predator population now aggregates in an area with higher pollen density (Fig. 4c1 and 5c), the over-all population growth will be higher, which, according to the apparent competition principle, will result in a lower herbivore density (Fig. 4c2 and 5c2). At high pollen supply levels, the herbivore is not driven to extinction as in the homogeneous case (Fig. 4a), but is suppressed to a level that asymptotically approaches zero with increasing pollen supply (Fig. 4c3). This is the result of the herbivores all seeking refuge in the area without pollen where a lower predator density can be found (Fig. 4c1, Fig. 5c2).

**Transient dynamics**

The system moves towards the equilibrium for a wide range of initial values, due to the extended invulnerable phase of the prey (Murdoch *et al.*, 1987; Abrams and Walters, 1996). The conclusions for equilibrium conditions, however, do not apply directly to the case of transient predator-prey dynamics, because now the growth-enhancement of the prey population (due to pollen-feeding by the prey), as well as the reduction of predation rate (due to pollen-feeding by the predator) come into play (chapter 3.1). If we consider the mean number of predator and prey (= herbivore) over the first 100 days, simulations for the case of a homogeneous environment show that there is an initial predator-density below which the mean herbivore density will be higher rather than lower in the presence of pollen (Fig. 6). This is because the herbivore initially profits from the pollen both by its increased reproduction and by a decreased risk of being eaten by predators. In this way, the herbivore initially has a higher population growth rate and therefore causes the plant to incur more damage in the presence of a supply of pollen. Above a critical initial predator density, the mean density of the predators will be higher in the presence of pollen, and that of the herbivore lower (Fig. 4b), which is qualitatively similar to the equilibrium case.

![Figure 6](image_url)

*Figure 6* The effect of initial predator population (adults released only) on mean herbivore density during first 100 days after predator release without pollen (thin line) and with pollen (thick line) supplied at different proportions of plant surface ($\alpha$). Initial herbivore population is 0.1/dm$^2$ with a stage distribution stable at unlimited growth ($a = 0.1 \cdot 10^4$ grains dm$^2$day$^{-1}$).
**The impact of supplementary food on a prey–predator interaction**

**Figure 7** The effects of predator distribution on (a) equilibrium herbivore distribution and density and (b) mean herbivore density during first 100 days after predator release, according pollen-herbivore-predator model. The dotted vertical line indicates the proportion of the environment supplied with pollen ($\alpha = 0.1$). Two herbivore distribution strategies are compared: even ($\beta = \alpha$) (thin lines, open dots) and flexible adaptive ($\beta$ according to eq. 13) (thick/intermediate lines, closed dots). Equilibrium results are presented for two pollen supply rates: $a = 0.1$ (thick lines) and $a = 0.3 \times 10^4$ grains dm$^{-2}$ day$^{-1}$ (intermediate lines). Dashed line indicates unstable equilibria. Dots indicate the (equilibrium or mean) adaptive predator distributions (when these exist). In (b) their ranges are indicated by horizontal lines. The dashed horizontal line indicates the (equilibrium or mean) herbivore level in a homogeneous environment with $a = 0.1$. In a homogeneous environment with $a = 0.3$ no equilibrium exists.
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In a split environment, one with and one without pollen, the critical predator density is shifted to much lower values (Fig. 6), and decreasing the area with pollen – while keeping pollen supply constant – further reduces mean prey density (Fig. 5b). These effects arise because (1) the predators tend to aggregate in the area with pollen, (2) the prey avoid the area with pollen to escape from the associated higher predation risk, and thus (3) the predator – not the prey – monopolizes pollen as a food source. Should the prey not avoid predators in the area with pollen (e.g. $\beta = \alpha$), even lower mean prey densities would be achieved (Fig. 7b).

Discussion

Perspectives for biological control

That supplementary foods such as nectar, sugar and pollen, can promote biological pest control, has been advocated for a long time (McMurtry and Scriven, 1966; Schiefelbein and Chiang, 1966; Kennett et al., 1979; Hagen, 1986; Van den Meiracker and Ramakers, 1991, McMurtry, 1992; Bakker and Klein, 1992). However, clear experimental evidence was still lacking. Our study has shown convincingly that supplying pollen can greatly improve the control of thrips with predatory mites in greenhouses. That this result is obtained in a system where both predator and herbivore can utilize the food source further widens prospects for application. Moreover, an accompanying model, parameterized on the basis of laboratory experiments, provide us with insight into the underlying mechanisms.

One crucial aspect is the distribution of alternative food supply. So far, little or no attention has been paid as to how to distribute alternative foods in a crop. Foods have either been dusted or sprayed to achieve a more or less even distribution (Ben-Saad and Bishop, 1976; Nichols and Neel, 1977; Hagley and Simpson, 1981), or they have been provided by introducing pollen- and/or nectar-producing ‘companion’ plants in the crop (Smith and Papacek, 1991; Hickman and Wratten, 1996; Ramakers and Voet, 1996). More recently, predators have been introduced together with alternative food (or non-target prey) via open rearing units positioned in the crop (Ramakers, 1990; Van Steenis, 1992). How these various ways of distributing alternative food affect the biological control of plant pests has not yet been considered. Our experiments show that the local supply of pollen on otherwise pollen-free cucumber plants increases the densities of predatory mites and suppresses the growth of the herbivore population even though the herbivore can also utilize pollen. Moreover, the analysis of our predator-prey model shows that uniform supply of alternative food leaves room for the herbivores to enhance their population growth rates and to escape from predator control, whereas local supply enables the predators to monopolize the alternative food source (Fig. 4-6).

Another much neglected aspect is the many and varied effects of supplementary foods on behavior and life history of predators. These foods may decrease predation on the target pest, increase survival, speed up development and promote reproduction. Moreover, they may cause retention of predators in the target crop. Which of these effects actually occurs, depends on the quality and quantity of alternative food. Some authors implicitly assumed that the effect of supplementary foods becomes manifest within one generation of the predator (Ben-Saad and Bishop, 1976; Nichols and Neel, 1977; Hagley and Simpson, 1981). They therefore ignored the impact of the foods on the predators’ reproduction and focus on the impact on predator survival and retention.
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Other authors considered the effects of supplementary foods over periods longer than a single generation, so that the predator's numerical response may have played an additional role (McMurtry and Scriven, 1966; Bakker and Klein, 1992). The importance of the latter is illustrated by our study on predatory mites and herbivorous thrips in a cucumber crop. Since our experiments were carried out in a greenhouse and with non-endemic predators, we can exclude attraction and retention of predators from outside the crop as a cause of improved thrips control. Thus, the positive impact of pollen results only from the predators' numerical response to pollen and thrips density. This numerical response apparently outweighs the negative effects of a decrease in the functional response and the accelerated population growth of the thrips due to feeding on pollen.

Evolution of plant-predator mutualism

Given that many plants produce edible pollen, we may now ask whether plants benefit even when the pollen is eaten by the herbivores as well. If we assume that (1) a single plant harbors a population of predators and herbivores obeying the equations of our model, that (2) the mean number of herbivores on a plant provides an estimate of plant damage and ultimately plant fitness, and that (3) much pollen will drop down on leaves of the same plant (and is thus wasted for the plant's reproduction), then the results of our model analysis can be viewed in an evolutionary context. We showed that the plant benefits from producing edible pollen via increased protection by predatory mites, even though the pollen can also be exploited by herbivorous thrips. This result critically depends on the ability of predators to increase their population growth rate by feeding on pollen. Under equilibrium conditions, utilization of pollen will always decrease the herbivore population, irrespective of whether pollen feeding promotes predator survival, development or reproduction, and irrespective of how the pollen is distributed over the plant. Under non-equilibrium conditions, however, the impact on the herbivore population depends not only on the benefit of pollen to the predator, but also on that to the herbivore via increased population growth rate and reduced consumption by the predators. Whether the overall effect on the plant will be positive or not, will thus depend on how pollen influences the predator-to-prey ratio near the moment of colonization of the plant by the herbivore, and the predator's numerical and aggregative response to herbivore density on the plant.

We showed that the benefits to the herbivore can be reduced if plants provide pollen locally. In doing so, the plant stimulates predators to aggregate near pollen sites, thereby increasing the predation risk to the herbivore that would forage for pollen, and reducing the benefits of pollen to the herbivore. Herbivores will be selected to avoid sites with pollen occupied by predators. Preliminary experiments indeed showed that thrips females avoid laying their eggs on leaves occupied by predatory mites (P.C.J. van Rijn, pers. obs.). In this way, the predators monopolize the alternative food source and achieve a higher population growth rate, thereby decreasing the herbivore population to even lower levels. However, from the plant's perspective predators should not be too strictly arrested at sites with pollen, because they would then lose their impact on the herbivores (Fig. 7). We therefore hypothesize that the secrets of the plant's indirect defenses (sensu Price et al., 1980) are hidden in how it manipulates the distribution and quality of pollen. This hypothesis might have more general implications for our insight in the various ways in which plants manipulate the third trophic level to their own benefit (Sabelis et al., 1999). Clearly, the plant may benefit from local supply, not only when it provides pollen, but also when it provides extrafloral nectar and protective structures (domatia). This might explain why extrafloral nectaries and mite domatia are found in specific areas (often near the leaf base) (Lundström, 1887; Bentley, 1977;
Walter, 1996), and why they are often functional only in a restricted (usually younger) part of the plant (Beattie, 1985).

Omnivory and food web composition

The 'predator' in our system feeds on herbivores as well as on plant material (pollen), and therefore represents a typical example of omnivory. As a consequence, the herbivore experiences both predation and exploitative competition by the predator, a combination that is called 'intraguild predation' (Polis and Holt, 1992). Although omnivory is now recognized as a widespread phenomenon (Polis and Strong, 1996), its ecological significance is still not fully understood. Simple model systems with omnivory are largely unstable (Pimm and Lawton, 1977, 1978). At low basal productivity levels, the predator cannot be maintained, and at high productivity the intermediate prey is eliminated due to apparent competition, leaving only a relatively small parameter domain where predator and prey can coexist (Holt and Polis, 1997; Mylius et al., 2001).

Holt and Polis (1997) list a number of mechanisms that may promote the coexistence of predator and prey. Recently, Mylius et al. (2001) have shown that one of these mechanisms - invulnerable prey stages in the prey or non-carnivorous stages in the predator - have only minor effects on the parameter domain where predator and prey can coexist. Our study now shows that another mechanism - adaptive behaviors in prey and predator in a spatially heterogeneous environment - greatly facilitate coexistence. When pollen occurs only in part of the environment, increasing pollen supply rate (technically similar to basal productivity) no longer results in full elimination of the prey, but only in suppression to low prey levels (Fig. 4ac). Bifurcation analysis of our model showed (Fig. 5c2) that predator and prey will coexist for any distribution of the resource (pollen) that slightly deviates from homogeneity (in our example \( \alpha < 0.98 \)). The underlying mechanism is that the basal resource is available in two qualities (in our case: leaf and leaf plus pollen) that are spatially separated, and that the predator concentrates more on the higher quality resource, thereby leaving a partial refuge for the prey at the lower quality resource. To prevent the elimination of prey, it is essential that at higher basal productivity levels the prey avoid the higher quality resource (\( \beta \to 0 \), Fig. 7a). When this is achieved by a flexible prey distribution, the predator should aggregate at the higher quality resource (\( \gamma > \alpha \), Fig. 7a). When, however, the predator aggregates too much on this resource (\( \gamma \to 1 \)), it no longer controls the prey population and no equilibrium exists (Fig. 7a).

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### Appendix A

**Population equilibrium**

When pollen density \((A)\) is fixed, and

\[
\phi A < \frac{N_0 (mg + \mu)}{g - (mg + \mu)}, \quad \text{and} \]

\[
N_1 + \phi A > N_\mu \Rightarrow \mu(N_1, A) \approx \mu_0 \quad \text{(as for the default parameter set)},
\]

the predator-prey model for a homogeneous environment has the following steady state:

\[
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\]
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\[ \dot{N} = \sum N_i = \left( \frac{d_i^{-1} + \tau + v^{-1}}{d_i^{-1}} \right) \dot{N}_i, \] where \( \dot{N}_i = \frac{N_i (mg + \mu_0)}{g - (mg + \mu_0)} - \phi A, \) and

\[ \dot{P} = \sum P_i = \left( \frac{e_i^{-1} + \tau + \mu_0 v^{-1}}{e_i^{-1} + \tau + \mu_0} \right) \left( \frac{R(A)}{v} - 1 \right) \frac{d_i}{f_N} \left( \dot{N}_i + \phi A + N_p + kA \dot{N}_i \right). \]

From the \( N_i \)-equation it can be seen that the prey equilibrium decreases linearly with increasing \( A \) until prey density has become zero.

When \( A \) is dynamic itself, or when the environment is subdivided, no explicit solutions for the population equilibrium are available. For these cases the equilibria have been studied with CONTENT 1.4 (a tool for bifurcation analysis).

Appendix B

Adaptive distributions of predator and prey over areas with and without pollen

When the per capita rate of migration out of an area is inversely related to the local effective food density (prey plus pollen), the proportion of predators in the area with pollen (\( \gamma \)) is described by the following ODE:

\[ \frac{d \gamma}{dt} = \frac{1 - \gamma}{(1 - \beta)N} - \frac{\gamma}{\beta N + \phi A}. \]

Assuming that redistribution is achieved at a shorter time scale than changes in population size, the actual distribution will be close to its pseudo equilibrium:

\[ \gamma = \frac{\beta N_i + \phi A}{N_i + \phi A}. \]

When the per capita migration rate of herbivores out of an area is inversely related to both the local effective food density (leaf plus pollen) and the local lifetime survival probability, the proportion of prey in the area with pollen (\( \delta \)) is described by:

\[ \frac{d \delta}{dt} = \frac{1 - \beta}{(1 - \alpha) N} \exp \left( -q(0) \frac{1 - \gamma}{1 - \alpha} P_c \right) \frac{\beta}{(\alpha L + A) \cdot \exp \left( -q(A/\alpha) \frac{\gamma}{\alpha} P_c \right)}, \]

where \( q(A') \) is the per-predator lifetime predation risk of the herbivores (the product of daily predation risk and mean duration of the vulnerable prey stage) at local pollen density \( A' \), which at low prey densities can be approximated by:

\[ q(A') = \lim_{N_i \to 0} \frac{F_N(N_i, A') \cdot d_i^{-1}}{N_i} = \frac{f_N \cdot d_i^{-1}}{Nf + \phi A'}. \]

At pseudo-equilibrium:

\[ \beta = \left[ 1 + \frac{(1 - \alpha)L}{\alpha L + A} \cdot \exp \left( -q(0) \frac{1 - \gamma}{1 - \alpha} - q(A/\alpha) \frac{\gamma}{\alpha} P_c \right) \right]^{-1}. \]
Since the pseudo-equilibrium distributions of predator and prey are mutually dependent and non-linear, they cannot be solved explicitly. To avoid this problem, only $\beta$ is calculated with its pseudo-equilibrium equation, whereas $\gamma$ is calculated by incorporating its ODE into the dynamical system.