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Persisting high predator-to-prey ratios and low prey levels: Model and experiments with thrips and predatory bugs

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Abstract Control by predatory insects has often been invoked as an explanation for why herbivorous insects occur at low levels and plants retain a green appearance. In many cases, however, herbivores possess invulnerable stages or have other methods to seek refuge. This would inevitably increase the abundance of the herbivores. We studied the dynamics of an arthropod predator-prey system consisting of the predatory bug Orius insidiosus and the western flower thrips, Frankliniella occidentalis, an herbivorous insect with eggs and pupae that are invulnerable to predation by Orius. Release of this predator on thrips-infested sweet pepper plants led to very low levels of thrips, and predator-to-prey ratios much higher than one. To explain this phenomenon a parameterised, stage-structured predator-prey model was explored mathematically. Bifurcation analysis showed that the persisting low prey levels and the high predator-to-prey ratios can only be explained by the presence of alternative food. These foods may well be of plant origin, especially because they benefit plants by promoting predators and thereby decreasing herbivores.

Keywords: Anthocoridae, Orius insidiosus, Frankliniella occidentalis, sweet pepper, predator-prey dynamics, refuges, invulnerable stages, alternative food, apparent competition, predation, biological control.

One of the most important challenges in population biology is to explain why predatory arthropods keep herbivorous arthropods at low levels, yet persist or stably coexist with their prey. The empirical basis stems from the observation that plants tend to retain a green appearance ('world is green' hypothesis; Hairston et al., 1966; Strong et al., 1984),
and from grand-scale experiences in classical biological control (Luck, 1990; Murdoch, 1992, 1994). These observations fly in the face of predictions from simple predator-prey models of the Rosenzweig-McArthur type, because they predict equilibria to become unstable when predators suppress their prey well beyond carrying capacity (Rosenzweig, 1971; Gilpin, 1972). The question, therefore, is which processes other than the ones in these classical models enable predator-prey systems to persist at low prey levels.

Theoretical explorations for the case of well-mixed, strongly coupled populations of predator and prey have shown by and large three possible mechanisms for stabilization of prey equilibria well below carrying capacity: (1) invulnerable prey stages (e.g. Thompson et al., 1982; Murdoch et al., 1987), (2) (partial) prey refuges (e.g. induced or constitutive plant structures; aggregative response of predators to prey density) (Hassell, 1978; Hassell and May, 1973; McNair, 1986, 1987; Sih, 1987; Murdoch et al., 1995), (3) positive density dependence with respect to the density of the target prey (switching; alternative food or prey) (Murdoch, 1969; Murdoch and Oaten, 1975; Oaten and Murdoch, 1975; Holt, 1977). Other such explorations for the case of spatially uncoupled predator-prey interactions (e.g. metapopulations) have shown that, given a large enough scale of observation, persistence at low overall prey levels is possible, even when local populations have unstable dynamics (Gilpin and Hanski, 1991; Hanski and Gilpin, 1996).

In this paper we studied a predator-prey system consisting of predatory bugs and herbivorous thrips. This system can persist for many generations in a greenhouse of less than 100 m². As this spatial scale is small relative to the flight capacities of the adults of thrips and predatory bugs, mechanisms operating at a metapopulation level are not likely to be of importance. Moreover, on a local scale, several features of this predator-prey system are known to have destabilising effects: age structure causing delays in numerical response of predators (de Roos et al., 1992; Hastings, 1983; Hastings and Wollkind, 1982; Gurtin and Levine, 1979; Smith and Mead, 1974) and concave functional responses (e.g. due to satiation) (e.g. Wollkind et al., 1982). One explanation for the observed persistence is the fact that some thrips stages are relatively invulnerable to predation. This decreased predation risk is caused by insertion of the eggs into leaves and pupation in the soil, away from the plant. Hence, the question to be answered is whether the invulnerability of some prey stages is sufficient to explain the observed persistence and predator-to-prey ratios, or that additional stabilising mechanisms (refuges for prey or alternative food for predators) need to be taken into account. Clearly, the existence of prey refuges should lead to increased prey equilibrium levels, whereas the availability of alternative food to the predator should lead to decreased prey equilibrium levels. The opposite effects of these two mechanisms can be used to make inferences on their relative importance. Here, we develop and analyse a model that takes age structure and the existence of invulnerable stages into account, but ignores prey refuges and alternative food for the predator. The predictions of this model are compared with the results of an extensive series of greenhouse experiments in which the dynamics of predatory bugs (Orius insidiosus (Say)) and western flower thrips (WFT, Frankliniella occidentalis (Pergande)) were recorded on sweet pepper plants (for a preliminary report see Van den Meiracker and Ramakers, 1991). Deviations from model predictions are then used to identify other stabilising mechanisms, and their influences are quantified by appropriate model extensions.
Population experiments: Material and methods

The experiments were done in a complex of greenhouses (76 m² each) separated by crop-free corridors (3.20 m width) serving as buffers. Each greenhouse contained 179 sweet pepper plants (*Capsicum annum*), grown on rockwool. Two sets of population experiments have been carried out, differing mainly in the period of the year: (1) from the end of April 1990 until mid November (cv. Evident; planting date December 13, 1989), and (2) from the end of January 1991 until the end of May (cv Mazurka; planting date November 7, 1990). These experiments are further referred to as the 'late season' and 'early season' sets of experiments. For horticultural reasons temperature minima in the late season experiments (17 °C at night and 21 °C during the day) differed somewhat from those in the early season experiments (before March 14, 15 °C at night and 25 °C during the day; after March 14, 19 °C at night and 21 °C during the day).

The late season experiments were initiated with either low, intermediate or high numbers of WFT in three separate greenhouses. These differences were created by releasing various amounts of adult thrips obtained from melon plants. One month later the thrips densities per 30 flowers were respectively: (1) 3 adults and no larvae, (2) 132 adults and 291 larvae, (3) 191 adults and 909 larvae. Two days after this prey assessment 500 young adults (3-7 days since final eclosion; c. 50% females) of the predatory bug, *O. insidiosus* (obtained from Dr. Ronald Oetting, Georgia, USA; reared on a diet of flour moth eggs at 25 °C), were released from a jar placed in the centre of each greenhouse. Part of these predators (16-27%) did not leave the jar, mainly males (c. 85%).

The early season experiments consisted of 2 replicates in separate greenhouses that were both started at low WFT densities (no initial WFT release; initial WFT densities much less than 1 larva and no adults per flower) with the release of 250 predatory bugs (3-7 days since final eclosion; c. 50% females) from a jar in the center of the greenhouse. About 9-16% of these predators (c. 63% males) did not leave the jar. In one of the two replicates there was spontaneous development of a WFT population, whereas this did not happen in the other. To test the resilience of the system to thrips invasion three releases of thrips (200 adults at the end of week 5, 6 and 7 since predator release) were carried out during the latter replicate experiment.

Population densities of WFT and predatory bugs were estimated in both sets of experiments from samples of 30 flowers, representing minimally 2% and maximally 10% of all the flowers. Upon picking, the flowers were instantly immersed in 50% alcohol to prevent escape of thrips and predators. After the flowers were rinsed, the insects were sieved out and counted. Such assessments were made initially once per week, and later – when density changes were small – once per two weeks. To determine the within-plant distribution of thrips and predators over flowers and leaves the late season experiments were extended with direct observations on the number of thrips and predators on one subapical leaf of each of 30 randomly selected plants. These leaf samples were taken at the end of week 6, 8, 10 and 12. To assess the between-plant spatial distribution in the greenhouse, the early season experiments were extended by inspecting all flowers for predatory bugs (end of week 1 and 4) and for adult thrips (end of week 4).

To prevent other sweet pepper pests from interfering with the experiments several measures had to be taken. For control of aphids (*Myzus persicae* (Sulzer)) the plants were sprayed with pirimicarb before predator release (only in the late season experiments), and the parasitoid *Aphidius matricariae* Haliday was released several times during the experiments. Despite these measures one corrective fumigation of pirimicarb was needed in the course of the late season experiment with low initial thrips.
Figure 1 Numbers of thrips (mainly WFT) (upper panel) and Orius insidiosus (lower panel) per sweet pepper flower in the late season experiments for high (a), intermediate (b) and low (c) initial WFT density. The arrow marks the moment of release of O. insidiosus. Solid lines with squares represent adults, whereas broken lines with dots indicate the juvenile stages. Open symbols indicate absence of predator or prey in the sample.
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density. Two-spotted spider mites (Tetranychus urticae Koch) were controlled by repeated release of the predatory mite, Phytoseiulus persimilis Athias-Henriot. In the late season experiments all greenhouses required one fenarimol treatment against powdery mildew, either in early August (high initial WFT density) or early September (the other two initial densities). Despite all these measures the late season experiment at high initial WFT density suffered noticeable damage from aphids and powdery mildew and had to be stopped at the end of August. These problems did not occur in the early season experiments.

Population experiments: Results

Late season experiments

Although the aim of the experiments was to study biological control of WFT, all late season experiments involved thrips populations that included other thrips species, mainly T. tabaci, as well. However, it is practically not feasible to identify the species in the juvenile stage. Therefore, percentage of T. tabaci in the adult phase was estimated in each population count. It appeared that the share of T. tabaci was very low (<5%) in the greenhouses with high and intermediate WFT density. In the greenhouse with low WFT density the share was initially very high, but decreased to 50% in the course of the experiment. The absolute number of adult T. tabaci was equally low in all three greenhouses. In what follows, we did not discriminate between the two thrips species, because they both represent herbivorous prey of not too different quality.

In the greenhouse with high initial WFT density the mean number of thrips larvae and adults increased from 36.7 to 42.6 per flower during the first week (Fig. 1a). In the second week thrips densities started to decrease and reached 6.0 per flower after three weeks; at that moment the O. insidiosus density had increased to 1.2 per flower (mainly nymphs). Thrips numbers further decreased until no more thrips were found in the flowers after six weeks. The O. insidiosus density reached a peak of 1.9 bugs per flower in the fifth week, and the population persisted after thrips had been eliminated from the flowers, and even till the end of the experiment. At the start of the experiment thrips was present in almost every flower, but absent after six weeks (Fig. 2a). From May to August the mean O. insidiosus density was 1.0 bugs per flower and the mean occupation in the flowers was 69%.

In the greenhouse with intermediate initial WFT density the number of thrips larvae and adults increased from 14.1 to 24.5 per flower during the first two weeks (Fig. 1b). But then a rapid decline occurred, one week later than in the previous experiment. From the sixth week onwards only a single thrips was found in the flower samples. The O. insidiosus population persisted to the end of the experiment in November (7 months); a peak density of 1.6 bugs per flower was observed after 8 weeks. Whereas initially thrips was present in almost every flower (Fig. 2b), flower occupation decreased sharply during the fifth week. From May till November the average O. insidiosus density was 0.8 per flower, whereas mean flower occupation was 62%.

In the greenhouse with low initial WFT density the number of thrips larvae and adults increased from 0.1 to 1.0 per flower during the first two weeks and then decreased to virtually zero (Fig. 1c). Occasionally, a thrips was found in the flowers from the sixth week onwards. Population build-up of O. insidiosus was slower than in the other two experiments, but eventually the density became similar, and reached a peak of 1.8
predatory bugs per flower after 8 weeks. Although mean numbers per flower were always low, thrips was present in up to half of the flowers during the first five weeks of the experiment (Fig. 2c). From May till November the average *O. insidiosus* density was 0.7 per flower, whereas on average 55% of the flowers were occupied.

Pooling the data in the period of leaf sampling (week 6 to 12) for all three experiments gave a mean *O. insidiosus* density of 1.2 bugs per flower and 0.2 bugs per leaf. In flowers, adults and older instars (IV-V) dominated (94%), while on leaves the younger instars (I-III) formed the majority (88%). In this period thrips was hardly found in flowers as well as on leaves. Additional observations with yellow sticky traps in October showed that some adult thrips were present in the greenhouse despite their virtual absence in flowers.

The population or tertiary sex ratio of both predatory bugs and thrips in the flowers was female biased in periods of high densities (87-90% in week 4 to 19 for *O. insidiosus* and 78-85% in the first five weeks for WFT).

**Early season experiments**

As these experiments were carried out in the period from January to May, invasions of native thrips species are unlikely. Indeed, other thrips species than WFT were not observed. Although there was no WFT released in this experiment, this thrips species occurred in very low densities in the course of the experiment. These thrips were probably brought with the plant material into the greenhouse, but overwintering in the greenhouse cannot be excluded.

![Graph](image)

**Figure 2** Proportions of flowers with (juvenile or adult) thrips (solid lines with squares) and (juvenile or adult) *Orius insidiosus* (broken lines with dots), in the late season experiments for high (a), intermediate (b) and low (c) initial WFT density. The arrow marks the moment of release of *O. insidiosus*. Open symbols indicate absence of predator or prey in the sample.
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Figure 3 Numbers of thrips (mainly WFT) (upper panel) and Orius insidiosus (lower panel) per sweet pepper flower in the early season experiments for two replicates (shown in 3a and 3b) with low initial WFT density. The arrows mark the moments of release. Solid lines with squares represent adults, whereas broken lines with dots indicate the juvenile stages. Open symbols indicate absence of predator or prey in the sample.

At introduction of *O. insidiosus* in replicate 1 (Fig. 3a), WFT was present in low numbers (less than one per flower). Next, WFT density increased slowly up to 3.1 per flower in week 6. Thereafter, thrips numbers decreased, whereas *O. insidiosus* reached a maximum density of 1.1 nymphs per flower in week 9 and 0.4 adults per flower in week 14.

At introduction of *O. insidiosus* in replicate 2 (Fig. 3b), neither in flower samples, nor on yellow sticky traps WFT was found. Subsequently, *O. insidiosus* increased. To assess the resilience of the low prey-high predator population state three WFT releases were carried out (in week 6, 7 and 8). None of these releases resulted in thrips densities higher than 0.2 per flower. *O. insidiosus* increased in numbers well before the WFT releases. Nymphal density peaked in week 9 and 14 (0.4 per flower), whereas adults peaked at 0.6 per flower in week 14.
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Figure 4 Distribution of plants with Orius insidiosus in their flowers in the early season experiments (two replicates): one week after introduction of the predators (a1, a2) and four weeks after their introduction (b1, b2). Each square represents a sweet pepper plant. The site of release is marked by R. Closed dots (nymphs) and closed diamonds (adults) represent observations of single individuals of the predators. Thrips adults (alive: open diamonds; dead: plus-signs) are only indicated in b. Note that thrips adults were not found in the second experiment (presented in b2).

Nearly all predatory bugs were found in crop rows adjacent to the release spot after 1 week in both replicate experiments (Fig. 4a). Initially, the spread within rows proceeded faster than between rows. After 4 weeks O. insidiosus nymphs (mostly 4th and 5th instars) were found in all crop rows in both replicate experiments (Fig. 4b). Because nymphs cannot fly and ambulatory dispersal is probably very limited, this rather homogeneous distribution of the older nymphs in the two greenhouses must have resulted from spread of the parental females within a much shorter period than 4 weeks (c. 2 weeks).

Fig. 4b1 (replicate 1) shows the distribution of plants with adult thrips and/or predatory bugs (nymphs and adults) in their flowers. In 60 plants only O. insidiosus adults or nymphs were found, whereas 34 plants had exclusively thrips in the flowers. Thus, most plants occupied by predatory bugs did not contain live thrips. In fact, there were only three plants with both predatory bugs and live thrips in their flowers. Thus, the
distributions of *O. insidiosus* and WFT are not independent (Fisher's exact test, two-tailed: \( p < 0.0001 \)) and show little overlap.

It should be mentioned that population experiments are open to invasion by other natural enemies. Hence, to interpret the results with care, we also recorded other enemies than released. Fortunately, such invasions happened in only one experiment where thrips were vanishingly low throughout the experiment: *Amblyseius cucumeris* (Oudemans) was found in low numbers after 6 weeks in replicate 2 of the early season experiment.

In conclusion, the early and late season experiments showed that irrespective of initial thrips density the release of predatory bugs ultimately led to a rather uniform picture: vanishingly low prey levels, and predator populations that persist at much higher densities (c. 1 individual per 2 flowers). Note that at low thrips levels thrips was absent in the samples in a considerable number of cases (see Figs. 1, 2 and 3, where absence is marked by open (instead of filled) symbols). Since only 2-10% of the flowers were sampled and (with one exception) no other parts of the plant, absence of thrips in the samples does not necessarily imply absence of thrips in the crop. Moreover, sticky trap catches in the end phase (*i.e.* October) indicated that thrips was present despite absence in the samples.

**Predator-prey model**

To analyse the population experiments, a stage-structured predator-prey model is made based on four simplifying assumptions: (1) interaction predominantly takes place in the flowers in a sweet pepper crop, (2) the ensemble of flowers represents a homogeneous interaction space, (3) populations of predator and prey are well mixed and (4) predator and prey populations are strongly coupled (no other natural enemies than the predatory bugs; no other prey for the predators). Whereas the first two assumptions are based on observed distributions over flowers and leaves, the other assumptions stem from the observation that, like the thrips, predatory bugs spread throughout the greenhouse within a generation time (Fig. 4). In addition of these general assumptions, three phases in the life of a thrips are distinguished based on reproductive activity and relative differences in vulnerability to the predators: (1) vulnerable non-reproductive phase (larvae), (2) invulnerable non-reproductive phase (pupae in the soil, young dispersing adults before the onset of egg-laying and in addition eggs inserted in the leaves), and (3) reproduction phase with intermediate vulnerability (ovipositing females). Note that the grouping of stages in phases (especially the egg stage as part of the second phase) is consistent with an interpretation whereby the larvae are conceived as the first stage (as it were, the adults are viviparous). The densities of the three phases are expressed as \( N_1 \), \( N_2 \) and \( N_3 \), respectively. Because the thrips densities considered are well below the plant’s carrying capacity (as is obviously desirable for biological control), 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 (thereby ignoring ‘doomed’ thrips as potential prey), whereas abiotic mortality in the mature phase is represented by a constant per capita rate (\( v \)) for the adults. By assuming constant per capita transfer (juveniles) and mortality (adults) rates, the time spent in each phase is exponentially distributed. This is a realistic assumption for the adults if one considers the shape of the net reproduction curve of the thrips (*i.e.* the product of reproduction and survival rates) (chapter 2.1), but not for the juveniles, where the time spent in the egg and larval phase
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is better approximated by a period of fixed duration when taking laboratory observations on developmental time into account. Hence, alternative models were analysed that are based on the assumption of a fixed residence time in each of the two juvenile phases. Clearly, fixed and exponentially distributed delays are two opposite ends of a continuum. In reality, distributions will take an intermediate position depending on spatial and temporal variability in leaf/flower quality and microclimate.

Biotic mortality of the thrips is assumed to be due only to predatory bugs and their predation rate is assumed to be linearly related to either prey density, or the square root of prey density, based on the following considerations. Van den Meiracker and Sabelis (1999) argued that the functional response cannot have a plateau in the range of realistic thrips densities (because the capture rate becomes zero only when the gut is filled to capacity). Using approximations given in Metz et al. (1988), the square root function is the most reasonable model for the predation rate ($F$):

$$F(D) = p_k \sqrt{D}$$

where $D$ is the density of vulnerable prey (thus either $N_l$ or $N_j$), $d$ is the rate of gut emptying, $m$ is the gut capacity and $b = g'(m)$, i.e. the differential of $g(s)$, where $g(s)$ is the rate constant of prey capture as a function of the level of gut fullness $s$ ($g(s)$ is zero at $s = m$). At low thrips densities and for small prey (relative to the predator’s gut capacity), however, the square root function does not hold because it is expected only when the predator reaches full satiation after each prey capture and subsequent ingestion event. A linear function is then expected instead:

$$F(D) = p_l D$$

where $g(0)$ is the rate of prey capture when the predator’s gut is virtually empty. Thus, depending on the degree of prey population suppression either of the above two types of functional responses (linear or square root) can be employed. The parameters of these functional response models depend on the developmental phase of predator and prey. For predation by adult predators the data can be found in Van den Meiracker and Sabelis (1999), whereas the relative difference in predation by juvenile predators is based on Isenhour and Yeargan (1981). These estimates are provided in Table 1.

As the parameters for the above formula are estimated for the case that $D$ expresses the density of second larval ($L_2$) stages of the thrips, whereas predation occurs on other stages as well ($L_1$, adults), additional assumptions are needed to translate the density of all vulnerable stages into functional and numerical responses. At sufficiently high thrips densities the predators will only partially ingest the content of their prey, so that $L_1$’s and adults effectively represent the same amount of food as the $L_2$’s. Since, in addition, the attack rates on the two larval stages do not differ very much, their densities are simply taken together, and the sum is represented by $N_l$. The attack rate on adult thrips, however, is 20% lower than that on the larval stages, according to closed cage experiments by Isenhour and Yeargan (1981). As this probably overestimates adult vulnerability (see discussion), the density of adult thrips is multiplied by a proportionality factor $h$ to account for the reduced attack rate relative to larval stages. These assumptions amount to the following formula for the weighted prey density:

$$D = N_l + hN_j$$

For reasons of simplicity this formula is also used for the case of low prey densities where the assumption on partial ingestion does not hold.
Table 1: Definitions and numerical values of parameters used in default predator-prey model. (See text for calculations and references; values based on observations at 25 °C).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description</th>
<th>Value</th>
<th>Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Prey (WFT) biology:</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( r )</td>
<td>net reproduction rate (ovipositional rate ( \times ) juvenile survival ( \times ) proportion females)</td>
<td>1.4</td>
<td>offspring-adult (^{-1}) day (^{-1})</td>
</tr>
<tr>
<td>( d_1 )</td>
<td>developmental rate vulnerable prey phase (larvae)*</td>
<td>1/6</td>
<td>day (^{-1})</td>
</tr>
<tr>
<td>( d_2 )</td>
<td>developmental rate invulnerable prey phase (eggs, pupae, pre-reproductive adults)</td>
<td>1/8</td>
<td>day (^{-1})</td>
</tr>
<tr>
<td>( \nu )</td>
<td>instantaneous decline rate net-reproduction rate</td>
<td>0.05</td>
<td>day (^{-1})</td>
</tr>
<tr>
<td><strong>Functional response:</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( p_L )</td>
<td>predation rate constant (linear functional response)</td>
<td>3.4</td>
<td>dm (^2) day (^{-1})</td>
</tr>
<tr>
<td>( p_R )</td>
<td>predation rate constant (square root functional response)</td>
<td>1.7</td>
<td>dm day (^{-1})</td>
</tr>
<tr>
<td>( f )</td>
<td>predation rate of nymphal predator relative to adult predators</td>
<td>0.8</td>
<td>(ratio)</td>
</tr>
<tr>
<td>( h )</td>
<td>vulnerability adult prey relative to larval prey</td>
<td>0-0.8</td>
<td>(ratio)</td>
</tr>
<tr>
<td><strong>Predator (O. insidiosus) biology &amp; numerical response:</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( e_1 )</td>
<td>developmental rate non-predatory phase (eggs)</td>
<td>1/5</td>
<td>day (^{-1})</td>
</tr>
<tr>
<td>( e_2 )</td>
<td>developmental rate predatory phase (nymphs)</td>
<td>1/13</td>
<td>day (^{-1})</td>
</tr>
<tr>
<td>( \mu )</td>
<td>instantaneous mortality rate adults</td>
<td>0.04</td>
<td>day (^{-1})</td>
</tr>
<tr>
<td>( c )</td>
<td>maximum rate of net reproduction (in absence of maintenance costs)</td>
<td>3.9</td>
<td>offspring-adult (^{-1}) day (^{-1})</td>
</tr>
<tr>
<td>( w )</td>
<td>maintenance costs (expressed in ( c ) equivalents)</td>
<td>0.9</td>
<td>offspring-adult (^{-1}) day (^{-1})</td>
</tr>
<tr>
<td>( k )</td>
<td>prey density at which reproduction is half it maximum (in absence of maintenance costs)</td>
<td>0.6</td>
<td>(prey dm (^{-2}))</td>
</tr>
</tbody>
</table>

* The total pre-mature period, \( 1/(d_1+d_2) \), is symbolised by \( D \). The duration of the vulnerable phase relative to the total pre-mature period, \( (d_1+d_2)/d_1 \), is symbolised by \( V \).

Incorporating mortality due to predation on each of the two prey phases separately \( (N_1 \text{ and } N_3) \) requires that the predation function \( F(D) \) is split in two terms: \( F_1 \) for the predation on \( N_1 \) and \( F_3 \) for the predation on \( N_3 \). For the case of a linear functional response this amounts to:

\[
F_1(N_1) = p_L N_1 \quad \text{and} \quad F_3(N_3) = p_L hN_3. 
\]

For the case of a functional response of the square root type this can only be done by a Taylor expansion of \( F(D) \) and neglecting higher order terms for \( h \) sufficiently low:

\[
F_1(N_1) = p_S \sqrt{N_1} \quad \text{and} \quad F_3(N_1, N_3) = \frac{p_S h}{2\sqrt{N_1}} N_3. 
\]

This approximation is acceptable as long as \( h N_1 \) is lower than \( N_1 \), a condition that is only critical in the end phase of diverging oscillations.

As in the thrips model, the predator’s life history is also divided in three phases, based on reproduction and feeding activity: (1) non-feeding and non-reproductive phase (eggs), (2) feeding and non-reproductive phase (nymphs and non-reproductive adults), (3) reproductive and feeding phase (adults).
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(3) feeding and reproductive phase (reproductively active adults). The densities of predators in each of these three phases are expressed as \( P_1, P_2 \) and \( P_3 \), respectively. Abiotic mortality in the juvenile phase (eggs and nymphs) is taken into account as an implicit reduction factor with respect to reproduction (thereby ignoring predation by the 'doomed' predators). This is a reasonable assumption because most juvenile mortality occurs in the first few days after egg hatching (Van den Meiracker, 1999). Abiotic mortality in the mature phase is represented by a constant per capita mortality rate (\( \mu \)) for the adults. By assuming constant per capita transfer (juveniles) and mortality (adults) rates the time spent in each phase is exponentially distributed. Whereas this representation is quite realistic for the adults, it is not for the juveniles. Hence, alternative models were analysed that are based on the assumption of a fixed residence time in each of the two juvenile phases.

The effect of thrips density on juvenile mortality and developmental time of the predators is ignored, whereas it is taken into account with respect to reproduction of the adults. This is done because the juveniles can meet their minimal food and moist requirements by feeding on plant juices or pollen. The effect of thrips density on reproduction is found by the following procedure. First, the mean gut fullness at a given thrips density is calculated by use of the Markov model described by Sabelis (1986, 1990) provided with estimates of gut capacity (62.4 mg) and the rate constant of prey capture, as a function of gut fullness (Van den Meiracker and Sabelis, 1999). Next, the rate of reproduction is calculated from the mean gut fullness using estimates of the minimum food requirements (i.e. 17 \( \mu \)g) and conversion efficiency (i.e. 4.9 \( \mu \)g food per egg) (Van den Meiracker and Sabelis, 1999). It appeared that the relation between the per capita rate of reproduction (\( G \) in eggs-female\(^{-1}\)-day\(^{-1}\)) and thrips density (\( D \), expressed in \( L_2 - \)thrips equivalents/dm\(^2\)), generated by the Markov model, can be fitted properly by a Monod function shifted over \( w \):

\[
G(D) = c \frac{D}{D + k} - w, \text{ or } G(D) = 0 \text{ when } D < \frac{kw}{c - w},
\]

where \( c = \) maximum rate of oviposition (in absence of maintenance costs) = 10.2 (eggs-female\(^{-1}\)-day\(^{-1}\)), \( k = 0.6 \) (\( L_2 - \)thrips equivalents/dm\(^2\)) and \( w = \) maintenance costs (expressed in egg equivalents) = 2.4 (eggs-female\(^{-1}\)-day\(^{-1}\)). The Monod function was fitted by eye to enable a good correspondence at low thrips densities at the expense of a slight underestimation of the maximum rate of reproduction. Both \( c \) and \( m \) are finally multiplied by the offspring sex ratio (0.5) and the juvenile survival (0.77) in order to obtain the net reproduction rate per adult (both male and female) (Van den Meiracker, 1999).

Taken together the above assumptions result in the following set of differential equations for the number of thrips \( (N_i) \) and predatory bugs \( (P_i) \) in each of their three phases \( (i = 1,2,3) \):

\[220\]
\[ \frac{dN_1}{dt} = rN_1 - F_1(N_1)(P_3 + fP_2) - d_1N_1 \]
\[ \frac{dN_2}{dt} = d_1N_1 - d_2N_2 \]
\[ \frac{dN_3}{dt} = d_2N_2 - F_3(N_1, N_3)(P_2 + fP_2) - vN_3 \]
\[ \frac{dP_1}{dt} = G(N_1, N_3)P_2 - e_1P_1 \]
\[ \frac{dP_2}{dt} = e_1P_1 - e_2P_2 \]
\[ \frac{dP_3}{dt} = e_2P_2 - \mu P_3 \]

Definitions and numerical values of the parameters are provided in Table 1. Explicit expressions for the equilibria are given in Appendix A.

Model predictions

Model predictions consist of (1) equilibrium values, (2) type of dynamics and (3) exact dynamical trajectory. However, the densities measured in the population experiments in the greenhouse are not directly comparable with the densities predicted by the model. This is because the sampling unit consisted of flowers, which are sufficient to determine population changes, but cannot be translated directly into total population sizes. For these reasons, prediction (1) and (3) cannot be validated. To circumvent this problem we used relative – instead of absolute – densities of predator to prey as the variables to be used in validation. The results show that the relative (predator-to-prey) equilibrium densities vary in the range of 0.5 to 1.4 (Table 2). Thus, it is predicted that predator densities are comparable to those of the prey.

To assess the type of dynamics, a combination of simulations and bifurcation analysis was carried out, using the above set of differential equations. Simulations were initialised by setting densities 10% away from their equilibrium value and were done using a 4th order Runge-Kutta integration method (for models with exponential delays) or a Euler integration method with a sufficiently small time step (0.025 day) (for models with fixed delays). Bifurcation analysis was performed using the Content software package (1.4) developed by Yu.A. Kuznetsov and V.V. Levitin at the Centrum voor Wiskunde en Informatica (CWI) in Amsterdam. As a default system a model version was selected with predation by juvenile and adult predators on larval prey only, exponentially distributed delays in development and a linear functional response, with parameter values as in Table 1. This default model has a stable equilibrium (Table 2). Note that stability is global (Fig. 5a), in part because the predator’s numerical response has a lower limit (reproduction cannot be negative). Below we explore how the stability of the equilibrium and how the type of dynamics is affected by realistic structural changes in this model.
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Table 2 Type of dynamics and predator-to-prey ratio at equilibrium of predator-prey model under different assumptions on the presence of alternative food, the shape of the functional response, the relative vulnerability of the adult prey (h), and the distribution of developmental delays.

<table>
<thead>
<tr>
<th>Model assumptions</th>
<th>Exponentially distributed delays</th>
<th>Fixed delays</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Functional response</td>
<td>Vulnerability adult prey</td>
</tr>
<tr>
<td>absent A = 0</td>
<td>linear</td>
<td>h&lt;0.092</td>
</tr>
<tr>
<td></td>
<td></td>
<td>h&gt;0.092</td>
</tr>
<tr>
<td></td>
<td>square</td>
<td>h&lt;0.035</td>
</tr>
<tr>
<td></td>
<td>root</td>
<td>0.035&lt;h&lt;0.041</td>
</tr>
<tr>
<td></td>
<td></td>
<td>h&gt;0.041</td>
</tr>
<tr>
<td>present A = 0.15</td>
<td>linear</td>
<td>h&lt;0.30</td>
</tr>
<tr>
<td></td>
<td></td>
<td>h&gt;0.30</td>
</tr>
<tr>
<td></td>
<td>square</td>
<td>h&lt;0.025</td>
</tr>
<tr>
<td></td>
<td>root</td>
<td>h&gt;0.025</td>
</tr>
</tbody>
</table>

1 at equilibrium (for lower value of h in range); 2 stable limit cycle; 3 diverging oscillations.

Predation on juvenile and adult thrips
The equilibrium is destabilised and limit cycles arise when both the juvenile and adult thrips are vulnerable to predation (Table 2). Thus, an increase in the number of vulnerable prey stages has a destabilising effect – in agreement with results obtained by others (Murdoch et al., 1987; Abrams and Walters, 1996). Bifurcation analysis showed that destabilisation of the equilibrium already occurs at low values of h (h > 0.092), the vulnerability of adult prey relative to juvenile prey (Fig. 5a). This is illustrated by stability domains in plots of h against various other parameters (Fig. 6a).

Square root functional response
If the functional response is changed from linear to square root, the equilibrium remains stable, but with a limited domain of attraction (Fig. 5b). However, when predation acts on both juveniles and adult prey (h > 0), the equilibrium becomes unstable when h > 0.035, with limit cycles for h < 0.041 or diverging oscillations for higher values of h (Fig. 5b, Table 2, Fig. 6b). In retrospect this result justifies linearisation by Taylor-approximation of the predation on adult prey, which holds only for low values of h.

Fixed delay
With fixed, instead of exponentially distributed, delays in development (Appendix B), the equilibrium becomes unstable and stable limit cycles arise (Table 2). When predation acts on both juveniles and adult prey (h>0), limit cycles become unstable when h > 0.026, resulting in diverging oscillations. Cycles also diverge when fixed delays are combined with a square root functional response (Table 2).

In conclusion, each of the above structural changes of the default model tends to destabilize the equilibrium.

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Figure 5 Bifurcation diagrams of \( P_3 \) against \( h \) for the default model with linear functional response (a) and a version including the square root functional response (b), indicating equilibrium values and minimum and maximum limit cycle values. A Hopf-bifurcation arises at \( h = 0.092 \) (in a) or at \( h = 0.035 \) (in b), after which stable limit cycles occur. In (b) a limit point cycle occurs at \( h = 0.041 \), and an unstable limit cycle (dashed lines) borders the domain of attraction of both the stable equilibrium and the stable limit cycle (drawn lines).
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Figure 6 Stability boundaries for the default version of the predator-prey model (see text, Appendix A and Table 1). All diagrams have $h$, vulnerability of adult prey, on the Y-axis, whereas the parameters along the X-axes are: (a1) $f$, the predation by nymphal predators relative to adult predators ($a_2$) $v$, the duration of the vulnerable phase relative to the total juvenile period, ($a_3$) $A$, the availability of alternative food to the predator. In addition, stability diagrams are presented for the case of a square root (instead of linear) functional response ($b_1$, $b_2$, $b_3$). Note the vertical in $a_3$ and $b_3$ at $A = 0.19$, which represents the marginal quality constraint on alternative food. A filled diamond indicates default parameter values. Diagrams of $h$ against the other parameters (not shown) can be qualitatively different, but they all support the conclusion that stable equilibria only occur at low values of $h$. 

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Discussion

Explanations for the observed high predator-to-prey ratios and predator persistence

The greenhouse experiments on predator-thrips dynamics show that – for varies crop seasons and initial thrips densities – the predatory bugs suppress western flower thrips to very low levels, and that populations of the predatory bugs undergo fluctuations, but persist throughout the season even when the density of thrips has become very low. The structured predator-prey model parameterised for this specific system served to test whether persistence of the predators at low levels of the prey can result from the stabilising effect of invulnerable stages (eggs and pupae). It was shown that – when developmental delays are exponentially distributed – the system can persist via limit cycles, but only when the functional response is linear, a case that is assumed to be realistic at the observed low equilibrial prey densities. However, when developmental delays are fixed, the predator-prey system will only persist (by way of limit cycles) when the vulnerability of adult prey is very low. Because fixed delays are more close to reality, the basic models cannot explain the predator persistence observed in our greenhouse experiments. Moreover, the basic models fail to predict the high predator-prey ratios observed in the greenhouse.

Hence, to explain these deviations between predictions and observations there must be mechanisms other than those included in the model. One way to promote persistence is to take into account distributed delays in development. Table 2 shows that exponentially distributed delays, when compared to fixed delays, promote persistence considerably. However, such exponential distributions represent one extreme, and fixed delays the other. In reality the distribution will be somewhere in-between, depending on temporal and spatial variability in host-plant quality and microclimate. Another possibility is that the vulnerability of adult thrips is much lower than expected on the basis of laboratory experiments (Isenhour and Yeargan, 1981). The experiments demonstrating vulnerability of adult thrips to predation were carried out in small and closed cages. In reality the adults have the possibility to jump and fly away in response to predator attack and they may even avoid sites occupied by predators (Van Rijn and Van Stratum, unpublished data). This will greatly reduce the impact of predation on adult thrips. Such a reduced vulnerability of adult thrips considerably increases persistence, as shown Table 2 and Fig. 6. For example, the model with a linear functional response and fixed developmental delays, produces limit cycles instead of diverging oscillations when the vulnerability of adult thrips is low \(k < 0.026\). Thirdly, prey refuges offer another powerful explanation for increased persistence (McNair, 1986). Possibly, part of the thrips population resides on the leaves (especially in periods of relatively high thrips or predator densities, see e.g. Shipp and Zariffa, 1991) where they experience a lower attack rate from the predators (see e.g. Shipp et al., 1992).

Additional modifications of the model are required to explain the observed high predator-to-prey ratios. None of the stability mechanisms referred to above can be of any explanatory value in this respect. Invulnerable adult prey and prey refuges will even increase prey equilibrium densities, whereas the predator-to-prey ratios are left unaltered or decrease. A higher predator-to-prey ratio can however result from: (1) higher population growth rates of the prey (which would mainly increase equilibrium predator levels [Oksanen et al. 1981]), (2) increased conversion efficiency or reduced maintenance costs of the predator (which would mainly decrease equilibrium prey...
levels), and (3) alternative food for the predator (which would mainly decrease equilibrium prey levels). The first two possibilities can be ruled out because the relevant parameters were implicit to the model’s predictions and will only produce clear predator biased predator-to-prey ratios when they deviate unrealistically from their estimated values. The presence of alternative food, however, offers a powerful explanation. Alternative food decreases the prey population at equilibrium and increases the equilibrium predator-to-prey ratio (even when the prey can utilise the alternative food as well; chapter 3.1). Most interestingly, this conclusion on the impact of alternative food still holds when the alternative food on its own is not enough to sustain a predator population (marginal quality constraint on alternative food). This can easily be demonstrated by representing the alternative food as a constant, $A$ (subject to the constraint), added to the prey density $D$ in the formula for the numerical response and by lowering the maximum rate of predation, $p$, assuming this food source to be non-depletable (Appendix D). In principle, the presence of alternative food can explain why the populations of *Orius* predators settle at a level much higher than the prey. Moreover, it increases predator persistence (Table 2, Fig. 6), albeit not enough to replace the stabilising mechanisms mentioned above. However, alternative food may further increase persistence when the predator exhibits density-dependent food preference (switching) (chapter 3.3) or when the food source is depletable.

**Does the alternative food originate from the plant?**

As our analysis points at a role of alternative food, the question arises whether there are candidate alternative foods. In the late season experiments in 1990, there were (phytophagous) arthropods that in principle could serve as alternative prey, such as the peach and potato aphids (*Myzus persicae*) and plant-inhabiting mites. However, their abundance was either always very low (mites) or increased to large numbers only in the last month of one of the late season experiments. In the early season experiments a role of alternative prey can be completely ruled out. However, there are good candidates of alternative foods that not of animal but plant origin: pollen, nectar, and possibly juices extracted from the leaf. Phytophagy is common among the Anthocoridae, although it depends on the type of plant, the type of food and the predator species (Naranjo and Gibson, 1995; Coll, 1998). Feeding on plant juices has been observed as they puncture leaves and increase their survival and in some cases even development (Askari and Stern, 1972; Kiman and Yeargan, 1985; Salas-Aguilar and Ehler, 1977; Coll, 1996; Fauvel, 1974). Another clear indication of a beneficial impact of plant feeding on the life history of anthocorids is observed on corn plants. Adults of *Orius insidiosus* feed on corn silks and the nymphs can reach adulthood on this food, but the adults emerging are smaller and less vigorous. Newly hatched nymphs start feeding on corn silks, but as development progresses, they tend to prefer thrips larvae as food. Extrafloral nectar of *e.g.* corn plants is known to attract various predators among which anthocorids (Yokoyama, 1978; Pemberton and Vandenberge, 1993) and the removal of these nectararies leads to a reduction in the abundance of predators (Schuster et al., 1976). Feeding on pollen occurs in many anthocorids. Some seem to feed almost exclusively on pollen (*Orius pallidicornis* (Carayon); Carayon and Steffan, 1959), others can complete development and oviposit on a diet of pollen, but also feed on prey (*Orius* spp. - Fauvel, 1974; *Orius insidiosus* - Dicke and Jarvis, 1962; Salas-Aguilar and Ehler, 1977; Kiman and Yeargan, 1985; McCaffrey and Horsburgh, 1986; Richards and Schmidt, 1996; *Orius sauteri* (Poppius) - Funao and Yoshiyasu, 1995; Zhou and Wang, 1989; Yano, 1996; *Orius laevigatus* - Frescat a and Mexia, 1995). Dissevelt et al. (1995) observed a pronounced difference in population development of various *Orius* spp. in pollen-
bearing crops (strawberry, eggplant, sweet pepper and melon), as opposed to crops without pollen (cucumber). Generally, anthocorids become more abundant in periods of increased pollen availability (Dickie and Jarvis, 1962; Isenhour and Yeargan, 1981; Isenhour and Marston, 1981; Mituda and Calilung, 1989; Coll and Bottrell, 1995). However, whether pollen and/or nectar from sweet pepper crops can be utilised by *Orius insidiosus*, is currently studied. Preliminary results suggests that sweet pepper pollen represents marginal food, as it allows for low reproduction and low juvenile survival (Van den Meiracker, unpublished data; Hulshof, unpublished data). Note that (1) also in the model the alternative food parameter was subject to a marginal quality constraint (*i.e.* no positive population growth in the absence of prey), but (2) still suffices to explain the observed high predator-to-prey ratios.

From an evolutionary perspective it is tempting to speculate on the benefits to the plant of providing foods that are accessible to the predators of herbivorous arthropods. Clearly, nectar and pollen have originally evolved for their role in plant reproduction and/or attracting pollinators. However, given that part of the pollen drop to lower leaves and nectar, exudates and plant juices are also provided extraflorally, one may wonder whether the accessibility, quality and quantity of these foods have been promoted by natural selection for plants that increase the efficiency of the third trophic level and manage to monopolise these benefits largely for themselves or their kin (Sabelis et al., 1999). Whether individual plants can gain the benefits, depends on the degree to which their neighbouring competitors profit as well and the extent to which plant-provided foods are used by other organisms that are not beneficial or even harmful to the plant. In this respect it is interesting to note that the western flower thrips can also utilise pollen. This does not necessarily disprove a mutualistic interaction between plants and the natural enemies of their herbivores, because mutualisms generally suffer from cheaters (Bronstein, 1994). Moreover, if pollen attract not only the predatory but also the herbivorous arthropods, then they cause the rate of predator-prey contact to increase, which may ultimately benefit the plant. In conclusion, there is room for a hypothesis on plant-predator mutualisms, but its final test will require more experimental work.

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**References**


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Appendix A

**Equilibria of model with exponential delays**

The predator-prey model with exponential delays mentioned in the text allows explicit expressions for the equilibria when the functional response is of the linear (instead of the square root) type:
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\[ N_1^* = \frac{k(\mu + w)}{c - (\mu + w)} \left( 1 + \frac{hp_L}{r} \right)^{-1} \]

\[ N_2^* = \frac{d_1}{d_2} N_1^* \]

\[ N_3^* = \frac{P}{r} QN_1^* \]

\[ P_3^* = \left( 1 + f \frac{\mu}{e_2} \right)^{-1} (Q - \frac{d_1}{p}) \]

\[ P_2^* = \frac{\mu}{e_2} P_3^* \]

\[ P_1^* = \frac{\mu}{e_1} P_3^* \]

where

\[ Q = \frac{1}{2} \left( \frac{d_1}{p_L} - \frac{\nu}{hp_L} + \sqrt{\left( \frac{d_1}{p_L} - \frac{\nu}{hp_L} \right)^2 + 4 \frac{r e_1}{hp_L^2}} \right), \text{ or } Q = \frac{d_1}{\nu} \frac{r}{p_L} \text{ when } h = 0. \]

For the case of square-root-type functional responses the expressions become too complex to provide direct insight, but it is possible to obtain numerical approximations. However, for the special case of negligible predation on adult thrips (\( h = 0 \)) explicit expressions can still be derived:

\[ N_1^* = \frac{k(\mu + w)}{c - (\mu + w)} \]

\[ N_2^* = \frac{d_1}{d_2} N_1^* \]

\[ N_3^* = \frac{d_1}{\nu} N_1^* \]

\[ P_3^* = \left( 1 + f \frac{\mu}{e_2} \right)^{-1} \frac{d_1}{p_L} \left( \frac{r}{\nu} - 1 \right) \sqrt{N_1^*} \]

\[ P_2^* = \frac{\mu}{e_2} P_3^* \]

\[ P_1^* = \frac{\mu}{e_1} P_3^* \]
Appendix B

Model with fixed delays

Incorporating fixed delays (cf. Gurney and Nisbet, 1983) for the juvenile phases in the master model, for the case that only $N_1$ is vulnerable to predation, yields the following set of delay-differential equations (DDE's):

\[
\frac{dN_1}{dt} = rN_1(t) - \frac{rN_1(t) + fP_2(t)}{N_1(t)} - \frac{rN_1(t - \tau_1)}{N_1(t)} s(t)
\]

\[
\frac{dN_3}{dt} = rN_3(t - \tau_1) s(t) - \frac{rN_3(t - \tau_1 - \tau_2)}{N_3(t)} s(t - \tau_2)
\]

\[
\frac{dN_3}{dt} = rN_3(t - \tau_1 - \tau_2) s(t - \tau_2) - \frac{rN_3(t)}{N_3(t)}
\]

\[
\frac{dP_1}{dt} = g(N_1(t))P_1(t) - g(N_1(t - \xi_1))P_1(t - \xi_1)
\]

\[
\frac{dP_2}{dt} = g(N_1(t - \xi_1))P_2(t - \xi_1) - g(N_1(t - \xi_1 - \xi_2))P_2(t - \xi_1 - \xi_2)
\]

\[
\frac{dP_3}{dt} = g(N_1(t - \xi_1 - \xi_2))P_3(t - \xi_1 - \xi_2) - \mu P_3(t)
\]

where $\tau_i = d_i^{-1}$ and $\xi_i = \epsilon_i^{-1}$. Note that the differential equations for $N_2$ and $P_1$ do not affect the dynamics of the system and are therefore put between brackets.

Defining the per capita death rate of the vulnerable prey at age $x$ as

\[
\delta(x) = \frac{F_1(N_1(x))(P_2(x) + fP_2(x))}{N_1(x)}
\]

the proportion of individuals in the vulnerable phase escaping predation becomes

\[
s(t) = e^{-\delta(t)}, \text{ where } z(t) = \int_{t - \tau_1}^t \delta(x) dx.
\]

When incorporated into a dynamic system, $s$ can be calculated from

\[
\frac{ds}{dt} = s(t)(\delta(t - \tau_1) - \delta(t)),
\]

with $s(0) = e^{-\delta(0)}$; as initial condition (Gurney and Nisbet, 1983).

However, modelled in this way, $s$ converged too slowly and consequently gave rise to erroneous results. We therefore used an alternative approximation for $s$, based on an idea of J.A.J. Metz (Leiden University, personal communication), by writing $\xi$ instead of $s$ as DDE:

\[
\frac{d\xi}{dt} = \delta(t) - \delta(t - \tau_1) e^{-\xi(t)} - \epsilon \xi.
\]

It can be shown that the integral of this differential equation converges to $\xi$ as defined above, provided that $\epsilon$ is sufficiently small.
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The equilibrium values for \( N_1, N_i \) and \( P_1 \) can be obtained by putting the differential equations to zero, ignoring time dependence of the variables. The equilibrium values for \( N_2, P_i \) and \( P_2 \) (required to calculate the predator-to-prey ratio) are proportional to those of the succeeding phases scaled by the relative mean duration of these phases (cf. the model with exponential delays). This leads to the following expressions for the variables at equilibrium:

\[
N_1^* = \frac{k(\mu + w)}{c - (\mu + w)} \\
N_2^* = \frac{\nu}{d_2} N_1^* \\
N_i^* = \frac{d_i}{\nu - r} \ln\left(\frac{\nu}{r}\right) N_1^* \\
P_1^* = \frac{\mu}{\epsilon_1} P_2^* \\
P_2^* = \frac{\mu}{\epsilon_2} P_1^* \\
\left[ F_1^* = \frac{\mu}{\epsilon_1} P_2^* \right]
\]

Appendix C

Equilibria with prey refuges

Two basic types of refuges are distinguished: (1) absolute number refugia and (2) proportional refugia (Hassell, 1978). In first case a constant number of prey will be inaccessible for the predator, which can be represented by subtracting a constant \( R \) from the number of (vulnerable) prey in the formula for the functional and numerical responses:

\[
F_1(N_i) = p_L(N_i - R) \quad \text{or} \quad F_1(N_i) = p_R\sqrt{N_i - R} \quad \text{and} \quad G(N_i) = c\frac{N_i - R}{N_i - R + k} - w.
\]

In the second case a fixed proportion of prey (\( q \)) will be inaccessible, which can be represented by multiplying the number of (vulnerable) prey by a positive fraction (\( 1-q \)):

\[
F_1(N_i) = p_L N_i(1-q) \quad \text{or} \quad F_1(N_i) = p_R\sqrt{N_i(1-q)} \quad \text{and} \quad G(N_i) = c\frac{N_i(1-q)}{N_i(1-q) + k} - w.
\]

Both types of refuges are used exclusively by the larval stages \( (N_i) \) and, compared to the outside world, they offer equal opportunities for development. The other phases \( (N_2 \) and \( N_3) \) are assumed to be invulnerable.

Incorporating these functions in the master model yield the following expressions for the equilibrium densities of the vulnerable prey and the adult predator, whereas the expressions for the other phases remain unchanged:
Case 1 (absolute number refugia):

\[ N_i^* = \tilde{N}_i + R, \text{ where } \tilde{N}_i = \frac{k(\mu + w)}{c - (\mu + w)}. \]

\[ P_i^* = \left(1 + f \frac{\mu}{e_2}\right)^{-1} \frac{d_1}{\nu} \frac{r-1}{F_i(\tilde{N}_i)} \tilde{N}_i \left(1 + \frac{R}{\tilde{N}_i} \right) \]

Case 2 (proportional refugia):

\[ N_i^* = \tilde{N}_i \frac{1}{1 - q}, \text{ where again } \tilde{N}_i = \frac{k(\mu + w)}{c - (\mu + w)}. \]

\[ P_i^* = \left(1 + f \frac{\mu}{e_2}\right)^{-1} \frac{d_1}{\nu} \frac{r-1}{F_i(\tilde{N}_i)} \tilde{N}_i \frac{1}{1 - q} \]

These equations show that prey refuges of both types increase the equilibrium densities of predator and prey, but do not affect the ratio of predator to prey.

Appendix D

Equilibria with alternative food

Alternative food is incorporated into the predator-prey model by adding a non-dynamic food source with an effective density, relative to that of the larval prey stages, represented by \( A \). This involves replacing the function for the ovipositional rate of the predator \( G(N_i) \) in the master model (and that for fixed delays in Appendix B) by:

\[ G(N_i, N_j, N_k, A) = c \frac{N_i + hN_j + A}{N_i + hN_j + A + k} - w. \]

This change will alter the equilibrium density for \( N_i \), whereas all other equilibrium densities are only affected through their dependence on \( N_i \). When only the first prey phase is vulnerable to predation,

\[ N_i^* = \frac{k(\mu + w)}{c - (\mu + w)} - A. \]

When additionally the adult prey phase is vulnerable to predation, the linear functional response case yields:

\[ N_i^* = \left(\frac{k(\mu + w)}{c - (\mu + w)} - A\right) \left(1 + \frac{hp_i}{r} Q\right)^{-1}. \]

Negative values of \( N_i^* \) are prevented by subjecting \( A \) to the marginal quality constraint (no positive population growth in absence of prey). These equations show that increasing \( A \) decreases the equilibrium prey densities, whereas the equilibrium predator
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densities are either not affected (when the functional response is linear) or decrease slower than the prey (when the functional response is convex). Thus, the effect of alternative food on reproduction will increase the predator-to-prey ratio. Other effects of alternative food, such as decreased predator mortality and predation rate, are incorporated by modifying parameter values. These increase equilibrium predator densities as well as equilibrium predator-to-prey ratios.