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The Impact of Supplementary Food on a Prey-Predator Interaction

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1.1

General introduction, outline and summary

Plant – carnivore mutualism

Plants may benefit from the presence of carnivores that attack the herbivores that feed on them. Plants may raise their benefit by improving the conditions for these carnivores e.g. by providing them with shelter, alternative foods, or information (Sabelis *et al.*, 1999). In this way an indirect plant defence system may develop, resulting in plant-carnivore mutualism. Plants are expected to provide these supplies only when the fitness benefits are on average greater than the costs, which will both vary with species and environment. Costs will not only result from the re-allocation of nutrients and energy, but also from the ‘misuse’ of the supplies by other, non-mutualistic organisms. This might result in a reduced share for the mutualists, but also in a better performance of organisms that actually harm the plants, such as herbivores. Other costs may come from a local diffusion of benefits to other, non-related, plants, which may enhance local competition. These costs, as well as the benefits in terms of reduced herbivory, are both dependent on the population-dynamical consequences of the supplies, and are ultimately affected by community structure.

In an attempt to unravel part of these complex population level feedbacks, I focus in this thesis on the consequences of plant supplies in a single plant-herbivore-predator chain where a food source provided to the predator is being ‘misused’ by the herbivore itself.

Plant-provided foods: extrafloral nectar and pollen

The plant-provided foods that are specifically addressed in this thesis are extrafloral nectar and pollen. Whereas extrafloral nectar is now generally considered as food that is provided by plants to improve their indirect defence, pollen is not. The main function of pollen is clearly to create offspring. Due to mate competition, however, it is often produced in large numbers, and consequently only a small proportion ends up on the stamen of another flower. The remaining pollen can still serve a second function as a food source for pollinators or carnivores. There are even plant species that produce two types of pollen: high fertility – low nutritious pollen and low fertility – high nutritious pollen, where the latter is hypothesised to serve mainly a mutualistic function (Wunnachit *et al.*, 1992). But also when no different types of pollen can be distinguished, selection, mediated by mutualists, might have affected the quality and quantity of the pollen. Edibility might be improved by e.g. reducing the thickness of the exine layer, and nutritional benefits might be improved by including amino acids or other nutrients that are limiting for the mutualists. Although more costly, also the amount of pollen produced might have increased due to its role in indirect defence. Selection for higher pollen production can especially be expected when pollen transfer is relatively efficient (and mate competition thus restricted), or when the mutualistic function competes with the sexual function because the mutualists already feed on the pollen before it’s transfer to other flowers.

The ecology and evolution of extrafloral nectaries (EFN) is relatively well studied, especially in relation to ants (Beattie, 1985). It includes the distribution of EFN among plant species and geographical regions, the seasonal and spatial distributions within the plant in relation to that of herbivores and ants, their production in relation to the presence of herbivores (Wäckers and Wunderlin, 1999), the chemical composition in relation to the needs and preferences of the mutualists (Wäckers, 2001), and most importantly, a quantification of benefits and costs for the plant (Beattie, 1985). The ecology and evolution of pollen, on the other hand, have mainly been studied in relation to its direct role in sexual reproduction, including the mode of transport (Faegri and Van der Pijl, 1979). That its role as a reward for pollinators might also have led to adaptations, both in shape and in number, is just beginning to emerge (Roulston and Cane, 2000; Cruden, 2000). Adaptation to its role as a food source for plant bodyguards has not yet been considered.

Entomologists, on the other hand, have recognised the importance of pollen as a food source for several groups of arthropods that might act as bodyguards. This includes heteropteran bugs (Alomar and Wiedenmann, 1996), ladybird beetles (Cottrell and Yeargan, 1998), hoverflies (Haslett, 1989), green lacewings (Sheldon and MacLeod, 1971) and predatory mites (McMurtry, 1992). It might even be used by some parasitoids (Jervis *et al.*, 1992). Some of these arthropods will act as a pollinator as well.

Apart from organisms that can benefit the plant, there are many organisms that utilise nectar and pollen without any return for the plant. For the nectar this includes several micro-organisms and commensal arthropods, such as fungivores. Other organisms feeding on nectar and pollen may even harm the plant, by e.g. herbivory or transmission of plant pathogens. For nectar this includes many lepidopteran and heteropteran pests (Rogers, 1985). For pollen this includes chrysomelid and curculionid beetles (Jayanth *et al.*, 1993; Jones *et al.*, 1993), lycaenid and *Heliconius* butterflies (Wagner and delRio, 1997; Gilbert, 1972), and many thrips species (Kirk, 1997). These costs of food provision can only be valued with proper knowledge of the behavioural and population-dynamical mechanisms involved.

The experimental system

The system under study in this thesis is a simple arthropod community that is artificially assembled on greenhouse grown vegetables for the biological control of its pests. The most prominent component is the western flower thrips, *Frankliniella occidentalis*. This species, which originates from the western part of North America, became a pest in the early 1980s, and then spread around the world (Brødsgaard, 1994). In the Netherlands it can survive inside greenhouses only. Here, it can feed on and cause serious damage to a wide variety of vegetable and ornamental crops. As indicated by its name, western flower thrips not only feeds on the cell content of green leaves but also, and preferably, on that of petals and pollen (Kirk, 1997).

Its invasion initially disrupted established biological control systems on especially cucumber and sweet pepper, where the main pests of spider mites and whitefly were successfully controlled by regular releases of a predatory mite (*Phytoseiulus persimilis*) and a hymenopteran parasitoid (*Encarsia formosa*), respectively (Van Lenteren, 1992). Also purely chemical control systems, common in most ornamental crops, were seriously contested by the western flower thrips, as this species showed high levels of pesticide resistance (Brødsgaard, 1994).

Shortly before the invasion of western flower thrips into Europe, it was discovered that certain phytoseiid mites (*Neoseiulus barkeri* and *N. cucumeris*), despite their small size, could effectively control the native onion thrips (*Thrips tabaci*) in cucumber

(Ramakers, 1980, 1983). These natural enemies showed some effectiveness against western flower thrips as well, and their use in pest control have been further developed and commercialized (Ramakers *et al.*, 1989). Later search for more effective predators have resulted in the use of one more mite species: *Iphiseius degenerans* (Van Houten *et al.*, 1996). All these three predator species have been subject to investigations reported in this thesis. Also several heteropteran insect species (*Orius* sp.) have been imported, and are effectively used for the biological control of thrips (see chapter 1.2). Van den Meiracker (1999) has studied the biology and population dynamics of one of these species (*Orius insidiosus*), and his results are further analyzed in this thesis.

Phytoseiid mites are smaller than thrips, and can effectively attack only the first larval stage of western flower thrips (Van der Hoeven and Van Rijn, 1990). *Orius* species, however, are larger than thrips and can attack all active thrips stages. The eggs of the thrips are inserted into the leaf tissue and the pupae reside in the soil) where they are largely invulnerable for both types of predators. All predators used for thrips control are generalist predators that feed not only on a variety of mite and insect prey, but also on pollen.

The main host plants used in these studies are cucumber (*Cucumis sativa*), and to a lesser extent, sweet pepper (*Capsicum annum*). In sweet pepper crops biological control of thrips require less introductions of predatory mites than in cucumber crops. One difference between these crops is that cucumber is replanted two or three times a year, whereas sweet pepper is replanted only once per year. Another difference is that sweet pepper displays continual production of flowers with edible pollen, whereas the commercially grown cucumber plants are parthenocarpic (develop fruits without pollination) and do not produce pollen.

Outline of the thesis and summary of results

The thesis is divided into three parts. Part One provides a general overview of predators of thrips and their potential to suppress thrips populations. Part Two describes laboratory experiments and modelling efforts concerning processes that take place at the *individual* level, whereas Part Three describes models and experiments at the *population* level.

Part one: introduction

In chapter 1.2 the capacity of prey suppression is reviewed for all known types of predators of thrips. This is done by using an extremely simple, analytically tractable, predator-prey model (the 'pancake model'), which helps to quantify the capacity of prey suppression and to categorise different types of dynamics following predator introduction into a crop. The predictions from this model were compared with experimental data available in literature and deviations from the predictions served to develop new hypotheses worth to be tested. One of these hypotheses concerns the impact of plant-provided food for the predators.

Part two: individual level

The basic biology of both thrips and predatory mites was studied in experiments presented in chapters 2.1 and 2.2. This included quantification of the developmental period of the different life stages and the oviposition and mortality rate in the adult stage, as well as estimating the intrinsic rates of population increase. The main message of chapter 2.1 is that on cucumber leaves *F. occidentalis* and *Thrips tabaci* have similar capacities for population increase. *F. occidentalis* is, however, the more severe pest on many different crops, and hypotheses were listed that might explain this discrepancy. One hypothesis is that *F. occidentalis* can use the floral resources, such as pollen, more efficiently.

This usage of pollen by *F. occidentalis* was further investigated in a separate study (not included in this thesis). The exponential weight increase during the larval period was shown to be 50% higher when cucumber leaves were provided with sweet pepper pollen, which resulted in a shorter juvenile period of the thrips when feeding on pollen. In the adult stage pollen feeding could almost double the daily reproduction compared to feeding on cucumber leaves only (as confirmed by Hulshof and Vänninen, 1999).

Chapter 2.2 showed that on a diet of pollen alone the predatory mites under study can reproduce at a rate that is equally high or even higher than on a diet of animal prey. This study also showed that not all pollen is suitable as food source for predatory mites, and that predatory mite species differ in the range of pollen species they can utilise as a food source. Extrafloral nectar affects the life history of predatory mites very differently from pollen, as shown in chapter 2.3. As it is mainly a source of carbohydrates and less of amino acids, extrafloral nectar alone did not allow the mites to develop or to reproduce, but it did allow the mites to survive much longer periods of prey absence than water alone, without losing their ability to reproduce when protein-rich food became available again.

To work out the population-dynamical consequences it is not only essential to assess the life history of the predator at ample supply of food, but also to determine how variation in prey density affects its predation rate and reproduction rate. These so-called functional and numerical responses are described in chapter 2.4, whereas the way these are affected by pollen feeding is addressed in chapter 2.5. The predation rate of predatory mites is not limited by prey handling, as traditionally assumed in functional response models (*cf.* Holling, 1959), but rather by the rate at which they digest and assimilate the consumed prey. By taking satiation as an internal state variable, and relating all components of the foraging process to the level of satiation, appropriate functional response models could be derived and parameterised for two pairs of predator and prey species. Comparing the predictions of these models with experimental results, it was concluded that the models correctly predict predation rates at high prey densities, but that at least one predator species (*N. cucumeris*) was more efficient in finding prey at low prey densities than predicted by the model, from behaviour observed at high prey densities. Apparently, prey density did not affect predator foraging via its effect on satiation only, and other state variables may have to be included.

To predict the effect of pollen feeding on the functional and numerical response of the predators, the predation model, described and parameterised in chapter 2.4, was extended to include feeding on a second food source (chapter 2.5). In contrast to the classic time budget models, the satiation-driven model predicted a plateau level of the functional response that was lower in presence of pollen. Predation experiments confirmed this pattern, as well as the unaffected plateau of the numerical response. The reason is that pollen feeding increases satiation beyond the level where the predator stops attacking prey. Since inclusion of satiation-driven models in higher-order population-dynamical models would seriously complicate their analysis, a modified version of Holling's time budget model is proposed that provides a qualitative description of observed functional response curves.

Part three: population level

In chapter 3.1 the results from part 2 have been brought together in a predator-prey model with the aim to predict how pollen affect the population dynamics of thrips and predatory mites, and to answer the more general question: will plants experience less herbivory when food is provided that can be eaten by both the predators and the herbivores? Greenhouse experiments in a cucumber crop with and without pollen supply were used to validate the model. These experiments, with *F. occidentalis* as herbivore

and the phytoseiid mite *I. degenerans* as predator, showed that in presence of pollen the predator population directly increased rather than declined, and that the herbivore population remained at much lower levels with than without pollen. A stage-structured predator-herbivore-pollen model showed this same transient pattern, but only after the space was split up in a leaf area with and a leaf area without pollen, over which both predator and herbivore were assumed to distribute themselves adaptively. Model analysis showed that the feeding by the herbivore on the supplementary food does not affect the equilibrium level. Since the supplementary food and the herbivore are consumed by and benefit the same predator, increasing the food level will decrease the equilibrium herbivore level, a principle termed 'apparent competition' (Holt, 1977). In the transient phase, however, the mean herbivore level can be higher when food is provided, when the initial number of predators is too low to prevent the herbivores to profit from the supplementary food. By concentrating the food in a smaller area of the plant, the predators will not only use the food source more efficiently, but will also deter the herbivores from the areas with food. As a result, providing food can profit the plant, both in the transient and in the equilibrium phase, even when it can also be eaten by the herbivores.

Chapter 3.2 analysed the impact of plant-provided food on another predator-prey system: with heteropteran predators (*Orius insidiosus*) instead of predatory mites. The model was parameterised based on data presented in another thesis (Van den Meiracker, 1999). The aim was to explain how it is possible that in greenhouse sweet pepper crops predator populations can persist with exhibit violent fluctuations, while prey populations remain vanishingly small throughout the experimental period, as observed by Van den Meiracker and Ramakers (1991). Mainly due to the larger size of the predator, the model differed from that of chapter 3.1 in that the vulnerable prey period is longer, predator development takes more time, reproduction and predation rates are higher and the functional response is non-saturating (linear or of square root type). The model analysis showed that the persistent high predator-to-prey ratios could only be explained by the presence of additional food for the predators (most likely pollen and floral nectar). In addition, the observed fluctuations could be explained by the limit cycles emerging from the predator-prey model, which suggests that the thrips prey (although rarely observed in the flowers) should still be present in the crop.

In the aforementioned models the predator displayed no preference for either of the food sources locally present, and showed a patch preference that is proportional to the relative local food densities. Optimal foraging theory, however, predicts a sudden switch in preferences when prey density increases beyond a threshold value. In chapter 3.3 the impact of this switching behaviour on the predator-prey dynamics was investigated in an unstructured Lotka-Volterra model with non-dynamic alternative food. The analysis showed that this type of switching does not stabilise the equilibrium, but may prevent unbounded oscillations and thus promote persistence. In the experimental system with thrips and predatory mites a stable equilibrium resulted from the long invulnerable period of the prey, and did not require additional mechanisms for persistence. The system with heteropteran predators, however, is expected to show limit cycles or even (when the predators attack adult thrips as well) diverging oscillations. Switching behaviour may therefore provide an explanation for the persistence of this system.

Implications for biological control

The theoretical and experimental results reported in this thesis showed that the provision of food to natural enemies of herbivorous arthropods can dramatically reduce the population levels of the herbivores and the related levels of plant damage. Providing

supplementary food to natural enemies in a crop, e.g. by spraying or intercropping, as a method to augment biological pest control, have been suggested and pursued many times, but has never been studied in great detail (Rogers, 1985; Baggen and Gurr, 1998; Mensah, 1997). This study (chapter 3.1) indicates the conditions required for this method to succeed.

First, the food should not necessarily be edible to the predators exclusively. When also the herbivores can use the food for reproduction, providing the food may still improve biological pest control, although additional conditions have to be met.

Second, the pest control may greatly improve when the supplementary food is provided on only part of the plant surface. By aggregating in these high-density food patches, the predators may use the food source more efficiently, and deter other organisms, including the herbivores, from using this food source.

Third, unless biological control can rely on predators immigrating from outside the cropped area, supplementary food can improve biological control only due to its effect on the numerical response of the predator within the crop. This implies that supplementary food will have no effect within one predator generation, and it should therefore be made available long before economic damage levels are approached. It also means that monitoring, aimed at checking the effects on herbivore levels and plant damage, should be extended beyond one generation after the onset of the food supply.

Apart from the artificial supply of alternative food for predators, one can also use plants that produce suitable food themselves. Because of the benefits advocated in chapter 3.1, it is worth looking for these bodyguard-supporting traits in plants and select and test species or varieties that express them.

More specifically regarding the control of western flower thrips, it was shown that providing cattail pollen enhanced population growth of the predators *I. degenerans*, and consequently reduced thrips populations to lower levels than without pollen supply (chapter 3.1). This showed that a predator species with relatively low predation and oviposition rates with thrips as prey (Van Houten *et al.*, 1995) can still be an effective biocontrol agent when augmented with the right supplementary food. Other studies showed that a predator species, such as *T. limonicus*, with relatively high predation and oviposition rates on a diet of thrips (Van Houten *et al.*, 1995), could still profit from additional food supplies (chapter 3.1). When however *N. cucumeris* was used, less clear results were obtained (unpublished results). Possible explanations are that (1) cattail pollen may not be a good food source for this predator when provided more than one generation, or (2) that this predator may not be sufficiently attracted to the leaves with pollen.

When larger predatory insects, such as *Orius* sp., are used rather than predatory mites, the thrips population is expected to go down much faster, as long as the same initial predator-to-prey ratios are provided (chapters 1.2 and 3.2). Supplementary food can in that case be used to help the predator population persist in the crop, thereby achieving long-term thrips control (chapter 3.2).

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