

WHEN DOES ALTERNATIVE FOOD PROMOTE BIOLOGICAL PEST CONTROL?

Maurice W. SABELIS¹ and Paul C. J. VAN RIJN²

¹Section Population Biology, Institute for Biodiversity and Ecosystem Dynamics
University of Amsterdam
Amsterdam, The Netherlands
sabelis@science.uva.nl

² Netherlands Institute of Ecology (NIOO-KNAW)
Boterhoeksestraat 48
6666 GA Heteren, The Netherlands
p.vanrijn@nioo.knaw.nl

ABSTRACT

That alternative food, whether or not provided by a plant or introduced artificially, promotes biological pest control via its effect on the predators, is not immediately obvious. On the one hand it enhances survival, reproduction and searching. On the other hand it may reduce the rate of predation, which is the case when alternative food and prey are substitutable – as opposed to complementary – food sources. Moreover, it is not immediately obvious how the impact of alternative food on the outcome of biological pest control differs depending on the type of dynamics (e.g., equilibrium vs. transient dynamics), the type of predator (e.g., stage-related consumption and life history effects of alternative food), the spatial structure of the environment (e.g., source-sink, metapopulation) and food web structure (presence of hyperpredators or intraguild predators). We review the conditions under which alternative food can lead to either prey/pest extermination, to a decline of the prey/pest towards a positive, asymptotic density or to no effect on prey/pest density at all.

INTRODUCTION

Carnivorous arthropods such as predators and parasitoids supplement their diet with plant-provided food (PPF), such as nectar or pollen. Depending on the arthropod taxa under consideration, this type of omnivory may occur in all or only in specific feeding stages. It usually stimulates survival, development and/or reproduction, thereby promoting the numerical response of the carnivore to the density of prey or host. Whether this numerical effect on the carnivore also translates in reduced prey/host densities, is not immediately obvious because consumption of PPF may negatively affect consumption of prey, because prey consumption and PPF consumption vary with life history stage, because prey and PPF vary in spatial distribution and because prey and PPF may be eaten by other members of the food web. Assessing the conditions, under which PPF reduces density at the second trophic level via its impact

on the third, is of crucial importance to designing strategies for biological control of crop pests.

Here, we summarize the results of theoretical exercises with consumer-resource models presented elsewhere (Van Rijn and Sabelis 2005). First, we consider the lessons from simple consumer-resource models that ignore stage or spatial structure. Second, we discuss results from stage-structured consumer-resource models to investigate how the impact of PPF on herbivory may depend on the life history and feeding requirements of the carnivorous arthropods. We compare parasitoids and predators, as well as predators with different types of omnivory. Third, we consider spatial structure and ask how the distribution of PPF and prey relative to each other matters to reducing herbivory. Finally, we step beyond consumer-resource interactions and ask when food web complexities (omnivory, hyperpredation, intraguild predation, competition) alter the predictions from simple consumer-resource models. All this will be discussed with a keen eye for how the theory can be applied to reduce crop damage by herbivores.

WELL-MIXED, UNSTRUCTURED CONSUMER-RESOURCE MODELS

To understand how PPF – through its effect on the carnivore – affects herbivore abundance, consider a system where a predator population directly controls a herbivore population, where individuals of each species are identical (e.g., no stage structure) and populations are well mixed (no spatial structure). These conditions apply to Lotka-Volterra or Rosenzweig-MacArthur models. The addition of PPF will initially result in an increase of the predator population, simply because there is more food available. This increase will come to a halt at equilibrium, i.e., when births exactly compensate for deaths. At this point, the herbivore population has decreased to an extent that compensates for the supply of PPF. Thus, adding food will lead to a decrease in the herbivore population via the consumers they share. This effect of a non-reproducing food source is very similar to the case where adding a second, reproducing prey species causes a decline of the first via the predator they share (Holt and Lawton 1994; Van Baalen *et al.* 2001; Van Rijn *et al.* 2002). The effect of one prey species on the other looks like competition, but in fact it is only apparent, because the mechanism is predator-mediated. This is why Holt (1977) termed it apparent competition, to create a contrast with resource and interference competition.

From the equilibrium equations of the one-predator-two-prey or predator-PPF-prey models, some counterintuitive conclusions emerge. If prey and PPF are substitutable food sources for the predator (Tilman 1982), addition of PPF will reduce equilibrium prey density, even when per capita consumption of PPF leads to a decrease in per capita consumption of prey. This insensitivity of the herbivore equilibrium to per capita prey consumption arises because equilibrium implies that the predators will increase to larger densities to achieve an overall prey mortality rate that compensates the overall prey birth rate. As long as the per capita predation rate exceeds zero, increasing the amount of PPF can even lead to extinction of the prey. At prey extinction, the predator population is maintained only by PPF. This prediction of prey extinction by adding PPF does not hold when food and prey are not substitutable, but complementary. Two food types are thought to complement each other when

they influence different components of the predator's life history. As an extreme example, consider the case where prey affects reproduction and PPF affects mortality. Then, increasing the amount of PPF also reduces herbivore density, but can never lead to extinction of the prey. This is because herbivore density declines asymptotically to a fixed level determined by background (= minimum) predator mortality.

As long as assimilation of PPF and prey will have a positive effect on predator reproduction and survival (which is why PPF should be eaten by the predator anyway!), PPF will reduce equilibrium prey densities irrespective of its effect on the prey consumption rate. Thus, it does not matter whether the predator switches to PPF at low prey densities or whether it becomes satiated for PPF at another level of ingested biomass than for prey (Van Baalen *et al.* 2001; Van Rijn, unpublished data). It even does not matter whether the herbivore consumes PPF and therefore survives, reproduces or develops faster (Van Rijn *et al.* 2002)! At equilibrium, the enhanced herbivore performance due to PPF will be compensated by predation from a larger predator population.

The equilibrium approach holds when environmental conditions, such as climate, availability of PPF to predators and plants to herbivores, remain unchanged over a sufficiently long period. How long the conditions need to be constant to approximate the equilibrium depends on the initial densities of the interacting populations, their generation times, and other traits of predator and prey that determine the dynamics around the equilibrium. For carnivorous mites and herbivorous thrips with generation times of about 3 weeks, populations were already within the 10% range of their equilibrium level after 12 weeks following their introduction in a cucumber crop (Van Rijn *et al.* 2002). After this period the impact of a regularly supplied food source on mite and thrips populations can adequately be predicted from equilibrium equations only. Arthropods larger than mites and thrips generally have longer generation times and their populations require more time to settle around the equilibrium (Sabelis 1992). For insects with only one or two generations per year and with food sources available only during part of the year, an equilibrium approach is unlikely to hold. In that case, one should rather focus on the dynamics displayed before the system approaches its equilibrium state (so-called 'transient' dynamics). Models of such systems require proper representation of developmental delays and age-dependent reproduction and this may make them mathematically less tractable. Although numerical techniques are available to simulate transient dynamics (Caswell 1989; De Roos and Persson 2001; Nisbet, 1997), obtaining transparent insight requires simplification.

We reduced complexity by focusing on the first generation after predator release (Van Rijn and Sabelis 2005). We assumed predators to be subject to a constant (i.e., herbivore-independent) per capita mortality rate, whereas the per capita prey mortality depends on predator density. Solving the integral over the first generation of the predators yields an expression relating prey density to background (= predator-independent) prey mortality, predation rate and predator mortality. If prey and PPF are complementary food sources, PPF may reduce predator mortality without affecting the predation rate. Then, reducing predator mortality by adding PPF translates into reduced prey density. If, however, PPF and prey are substitutable, then adding PPF may reduce predator mortality as well as predation rate. To make herbivore density go down requires that PPF reduces predator mortality more than it

reduces the predation rate. If PPF is not only utilized by predator, but also by prey, adding PPF as a complementary food to prey will only reduce herbivore density when its reducing effect on predator mortality is disproportionately larger than that on background prey mortality. This demand will be even more extreme when substitutability of foods is assumed and therefore consumption of PPF will likely go at the expense of that on prey. Thus, for prey density to go down in the first generation after predator release adding PPF is subject to stringent conditions. It is then critically important to know whether foods are substitutable or complementary and whether herbivores utilize PPF as well. These conclusions are quite complex, yet they are intuitively much more obvious, than the simple general conclusion drawn for the case of equilibrium conditions stating that: PPF always reduces herbivore density irrespective of its effect on predation and irrespective of its utilization by the herbivore.

STAGE-STRUCTURED CONSUMER-RESOURCE MODELS

Real-world predator-prey and parasitoid-host interactions differ in the life stages that are affected by prey (or host) density and/or PPF. In general, three scenarios can be observed that differ in whether (A) adult performance (survival, attack, oviposition), (B) juvenile performance (survival, development) and (C) both adult and juvenile performance are affected by prey density. The different types of PPF (nectar, pollen) can also have three different effects as it may (1) promote survival, (2) provide fuel (when rich in sugars as in nectars) for searching and (3) enhance assimilation processes (when rich in amino acids as in pollen), and thereby development and oviposition. As defined above, PPF and prey can be substitutable or complementary food sources and they are called essential if their absence causes the carnivore population to decline even at the highest abundance of the other food source (i.e., reproduction does not compensate mortality or the basic reproduction ratio $R_0 < 1$). Assuming the prey/host is always essential, PPF is never essential when substitutable, but when complementary it can be either essential or not.

Scenario A applies to parasitoids. Here, the larva is carnivorous. It feeds in or on a single host. So there is no need to search for hosts. The adult female searches for hosts and she makes decisions on whether to lay eggs in hosts. Usually the adult female feeds on PPF, but some species also feed on hosts. Thus, host density affects the oviposition rate of the adult parasitoid, but not the survival or development of the larvae. Scenario B comes close to hoverflies. Here, the purely carnivorous larvae actively search for prey, whereas the adult females feed on PPF and lay eggs near areas with prey. Thus, prey density will here most strongly affect juvenile performance. Scenario C is best illustrated by ladybeetles, predatory bugs, earwigs and predatory mites, where carnivory and search for prey occurs in all active stages. Here, prey density will affect the juvenile, as well as adult performance. Lacewings have always actively searching larvae, but some species are carnivorous as adults and other are not. Thus, they represent either scenario B or C. If the oviposition rate of hoverflies strongly depends on how much prey the area harbours, then they are more close to scenario C than to B. Scenario C also becomes more applicable to parasitoids when they kill and feed on hosts to obtain nutrients essential for egg maturation.

For each of the three scenarios on stage-related prey density dependence models were developed that incorporate the effect of substitutable or complementary PPF affecting (1) survival, (2) searching or (3) development and reproduction, plus any combination of 1, 2 and 3. Parameters ranges were based on literature data. From the equilibrium equations of those models we derived how equilibrium prey density changes with an increase in PPF. Such calculations are particularly meaningful when populations return to the equilibria after perturbation (i.e., equilibria are stable). This is likely when not all prey stages are vulnerable to predator attack (Murdoch *et al.* 1987), which holds for many arthropod predator-prey systems (Sabelis 1992; Sabelis and Van Rijn 1997). These calculations show that increasing PPF – whether substitutable or complementary, essential or not essential – causes equilibrium prey density always to decline under all scenarios, but the mode and quantitative details of the decline depend on the scenario under consideration. Extinction above a critical level of PPF availability can only be achieved when the predators eat PPF and prey as substitutable foods in all life stages (and are thus true omnivores) whereas both mortality and reproduction are affected by PPF. In all other cases increasing PPF can never drive the prey population to extinction. Instead, prey density will asymptotically approach some positive value set by the level of background (= minimum) predator mortality. Under each of the three scenarios (A, B and C) the strongest decline in prey density is achieved when PPF is substitutable (and hence non-essential) and when PPF promotes both survival and reproduction of the predator; effects of PPF on survival alone come second in prey suppression efficiency and effects of PPF on searching alone come third. When PPF is essential (and hence complementary), there is a minimum amount of PPF required for the predator population to persist and thereby to suppress the prey population.

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SPATIALLY STRUCTURED CONSUMER-RESOURCE MODELS

The models discussed above are based on the assumption that predators, herbivores as their prey, and food plants of the herbivores are well mixed and therefore do not take the spatial component of predator-prey interactions into account. This assumption is valid as long as the grain size of the spatial heterogeneity is well below the average foraging range of the consumers. In many cases, however, this assumption does not hold. When herbivores as prey and their food plants co-occur only at spatial scales that are beyond the search range of individual predators, new mechanisms may come into play that are absent in fine-grained environments: predator aggregation, spatial subsidies, and metapopulation dynamics.

Suppose there are two types of sites, plants with herbivores as prey and plants providing alternative food (PPF). When the two plant types occur sufficiently close together, or even merged into one plant species harbouring sites with PPF and sites without, predators may disperse fast enough to achieve a distribution proportional to the amount of food (prey and PPF) on those sites (so called Ideal Free Distribution). Suppose Rosenzweig-MacArthur models govern predator-prey dynamics on each of the two sites and the predators distribute themselves ideal free over the two sites (Van Rijn *et al.* 2002). Then, for a constant PPF supply the predator distribution stabilizes at equilibrium. The more PPF, the stronger the predators

aggregate at the PPF site and the stronger the suppression of herbivores at this site, whereas the suppression in the PPF-free site is weak. Decreasing the area of the PPF site relative to the total area intensifies the impact on herbivore density in this area, but leaves the herbivore density in the non-target area unaffected (Van Rijn and Sabelis 2005). Thus, target sites or plants can be protected against herbivory by arresting predators with the aid of alternative food (PPF). The mode of decline in herbivore density (linear decline to extinction or asymptotic decline to constant level) will be much like those observed in the models of well mixed populations and thus depend on whether PPF and prey are substitutable or complementary, essential or non-essential foods. This local indirect effect of PPF on the herbivores via dispersal of the predator is comparable with 'apparent (predator-mediated) competition', but as it results from behavioral rather than life-history responses, it acts already on time scales shorter than a generation, and has therefore been termed 'short-term apparent competition' (Holt and Kotler 1987). Clearly, this short-term effect of PPF will work most effectively when large areas of (semi)-natural habitat surround agricultural fields and have low numbers of potential pest organisms and some redundancy in the carnivorous species feeding on the pest organisms.

When plants with PPF and those without are further apart, the plants with PPF may subsidize the predator population on PPF-free plants, and help to suppress herbivore numbers there. This represents a source-sink system at the landscape scale (Dunning *et al.* 1992; Polis *et al.* 1997; Pulliam 1988) and can be modelled by two Rosenzweig-MacArthur, predator-prey models, one for the source and one for the sink, that are coupled by dispersal. The impact of PPF via the predators on herbivores on the distant PPF-free plant will vary depending on whether PPF and prey are substitutable or complementary, essential or non-essential. If PPF in the source habitat is complementary and essential yet absent in the sink habitat, it may contribute to suppression of herbivores in the sink habitat (even though here – following the definition of a sink – predator reproduction does not cancel out mortality). When PPF is non-essential, the predator population can persist anyway and by definition the PPF-free habitat cannot be a sink. The habitat with PPF will harbour fewer herbivores and more predators, causing dispersal into the PPF-free habitat. Here, the impact on herbivore density is less pronounced, however, than if PPF is essential. When PPF and prey are substitutable, herbivore density is reduced in the habitat with PPF to a level that exactly compensates for the amount of PPF available. Hence, predator density in that habitat remains unaltered and there will be no net migration into the PPF-free habitat and, hence, no change in prey density. If, however, PPF availability is such that it just supports the predator population and drives prey extinct, any further increase in PPF availability will no longer be compensated by a decrease in prey density, but will translate directly into a larger carnivore population. Predators dispersing into the PPF-free habitat will now cause herbivore density to decrease.

For many real-world systems of arthropod predators and their prey, equilibria may not be feasible. Sources may turn into sinks and vice versa depending on the season or local predator-prey dynamics is intrinsically unstable. In some acarine predator-prey systems in orchards PPF (e.g., pollen) emerging early in the growing season plays a critical role in building up a predator population large enough to suppress the prey population later in the year. In other acarine predator-prey systems predators tend to overexploit their prey and then disperse aerially to find new prey patches (e.g., Pels and Sabelis 1999; Pels *et al.* 2002; Sabelis and

Van der Meer 1986). Here, PPF may either alter the outcome of transient dynamics in local predator-prey populations or it may provide indispensable fuel for dispersal. According to metapopulation models of the patch-occupancy type (Levins 1969) increased rates of dispersal due to PPF will result in a decrease of the number of prey patches. If, however, PPF promotes the within-patch per capita growth rate of the predators this is likely to result in earlier prey extermination and lower numbers of predators that disperse from a patch. This implies a lower dispersal predator dispersal rate and hence an increase of the number of prey patches in the metapopulation. Thus, to understand the metapopulation consequences of PPF it is critical to assess how it influences between-patch predator dispersal as opposed within-patch predator-prey dynamics.

DISCUSSION: BEYOND CONSUMER-RESOURCE MODELS

In this article we provided a review of the conditions under which PPF gives rise to herbivore suppression via a shared consumer. In particular, we considered how the impact of PPF is modified by stage- and space-related interactions. With few exceptions, the overall pattern is that PPF somehow promotes herbivore/prey suppression. The underlying assumption was that the system consists of one species at the third trophic level, one species at the second trophic level and PPF, as an influence from the first trophic level. In reality, herbivore and carnivore are part of a much more complex food web of species interacting with each other, (Polis and Strong 1996). How will these interactions affect the conditions under which PPF leads to herbivore suppression?

Consider first the presence of a fourth trophic level. Carnivores may have their own suite of (hyper-)predators, (hyper-)parasitoids, and pathogens (Rosenheim 1998; Sullivan and Volkl 1999). Trophic cascade models predict that the top-carnivore will at equilibrium control the primary carnivore, so that the herbivore is released from top-down control (Oksanen *et al.* 1981). The equilibrium density of the primary carnivore would be determined by the traits of the top-carnivore, whereas the herbivore would grow to a density where it is limited from bottom up. This implies that at equilibrium, food provided to the primary carnivore would no longer affect the density of the primary carnivore, nor that of the herbivore! In some cases, PPF can (also) be used by the top-predator or hyperparasitoid (Chang *et al.* 1994). PPF will now likely reduce the density of the primary carnivore, and consequently have a negative rather than a positive impact on biological control of the herbivores. Thus, the presence of a fourth trophic level may dramatically alter the predictions for the impact of PPF on herbivore suppression.

At the third trophic level, competition for herbivores as prey and intraguild predation may alter the species composition and thereby the impact on herbivore suppression (Polis and Holt 1992; Polis *et al.* 1989; Rosenheim 1998). PPF may change the outcome of competition and intraguild predation by promoting one species more than others (e.g., Evans and England 1996). If PPF supports the species that in absence of PPF is a worse competitor but a good intraguild predator, PPF may reduce the density of the better competitor and promote herbivore density (Briggs and Collier 2001; Holt and Polis 1997; Hunter *et al.* 2002; Mylius *et al.* 2001; Rosenheim 2001; Rosenheim *et al.* 1995; Snyder and Ives 2001). However, beyond the PPF level that results in exclusion, PPF will have the same effects as predicted from simple

carnivore-herbivore models. Thus, rather restrictive conditions are required for competition and intraguild predation to alter the predictions for the impact of PPF on herbivore suppression obtained from simple predator-prey models.

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