22

Evolution of Exploitation and Defense in Tritrophic Interactions

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22.1   Introduction

Why do plants cover the earth and give the world a green appearance? This question is not as trivial as it might seem at first sight. Hairston *et al.* (1960) hypothesized that herbivores cannot ransack the earth of its green blanket because they are kept low in number by predators. They tacitly ignored the possibility that plants defend themselves directly against a suite of herbivores and together exhibit such great diversity in defense mechanisms that "super" herbivores able to master all plant defenses did not evolve and those that overcome the defenses of some plants are limited by the availability of these plants. Strong *et al.* (1984) recognized both possibilities in their review on the impact of herbivorous arthropods on plants, but they also favored the view that predators suppress the densities of herbivores, and thereby reduce the threat of plants being eaten.

The two explanatory mechanisms (plant defense versus predator impact), however, may well act in concert. Ever since the seminal review paper by Price *et al.* (1980) ecologists have become increasingly aware that plant defenses include more than just trickery to reduce the herbivore's capacity for (population) growth. For example, the plant may provide facilities to promote the foraging success of the herbivore's enemies. This form of defense is termed *indirect* as opposed to direct defense against herbivores. Examples of direct defenses are:

■ Plant structures that hinder (feeding by) the herbivore (e.g., cuticle thickness, "smooth" cuticle surfaces that do not provide a holdfast, impenetrable masses of leaf trichomes, glandular trichomes acting as sticky traps);
■ Secondary plant compounds that modify the quality of ingested plant food (digestion inhibitors), intoxicate the herbivore, or signal the plant's well-defended state to "discourage" the herbivore (feeding deterrents).

Indirect plant defenses bypass the direct defense route against the second trophic level by promoting the effectiveness of the third. For example, plants may retain the herbivore's enemies by providing protection and/or food and they may attract these enemies by betraying the presence of prey via herbivory-induced chemical plant signals. When Price *et al.* (1980) published their review paper, certain ant–plant interactions provided the best-known examples of indirect defenses [Janzen

1966; Bentley 1977; see also reviews by Beattie (1985) and Jolivet (1996)]. Now, more than 20 years later, it has become increasingly clear that the conspiracy between plants and predators against herbivores is a widespread phenomenon; a wide range of plants from many different families invest in promoting the effectiveness of a suite of predatory arthropods (Beattie 1985; Buckley 1986, 1987; Dicke and Sabelis 1988, 1989, 1992; Dicke *et al.* 1990; Koptur 1992; Drukker *et al.* 1995; Takabayashi and Dicke 1996; Turlings *et al.* 1995; Jolivet 1996; Walter 1996; Scutareanu *et al.* 1997; Sabelis *et al.* 1999a, 1999b, 1999c, 1999d).

In this chapter, we outline how analysis of the way plants defend themselves against herbivores can shed light on certain issues in host–parasite interactions. Many analogies exist between plant–herbivore interactions and host–parasite interactions. In fact, arthropod herbivores can easily be considered as "parasites" of the plants: compared to their host they are small, and the detrimental effects incurred result not so much from the effect of a single herbivore, but rather from the combined effects of the population that develops. Thus, it is in the interest of the plant to slow local herbivore dynamics as much as it is in the interest of an animal host to block within-host parasite dynamics. As argued above, plants may do so by direct means of defense, but they may also solicit the help of the predators of the herbivores. Thus, predators may function effectively as a kind of "immune system" for the plants. Insights into plant–herbivore–predator interactions may therefore provide clues to understand evolutionary aspects of host–parasite interactions. Our approach, as it is explicitly based on models for local population interactions between herbivore and predator, can be used to assess how, by changing certain parameters, the plant can manipulate the interaction to its own benefit. We use this approach not only to expose the game-theoretic aspects of the interaction between trophic levels, but also the interactions *within* these levels. Local competition among predators or herbivores has a clear link with the evolution of virulence, as this can also be strongly affected by within-host competition (Nowak and May 1994; Van Baalen and Sabelis 1995a).

We treat the system as a simple linear food chain of plants, herbivores, and predators, and hence ignore the many and varied ways of "cheating and misusing" that exist in complex food webs of arthropods on plants. We prefer to concentrate here on the evolution of food exploitation strategies of the herbivores and predators in response to investments in direct and/or indirect defenses on the part of the plant. Typically, herbivorous arthropods may (evolve to) be mild or malignant parasites of the plant and predatory arthropods may (evolve to) be prudent or wasteful exploiters of the population of herbivorous arthropods on a plant. Clearly, for a plant to invest in direct and/or indirect defense, it matters how virulent the herbivorous arthropods are to the plant and how virulent the predatory arthropods are to the population of herbivores on a plant. We argue that, to understand the evolution of mutualistic interactions between plants and the natural enemies of herbivorous arthropods, we should identify the advantages to the individual plant and the individual predator, predict the consequences for the population dynamics of herbivorous and predatory arthropods, and elucidate how dynamics in turn

affects the evolution of plant–predator mutualism and the herbivore's response to this conspiracy. Whereas a definitive solution is not within reach, we hope to convince the reader that there are many possible outcomes for the evolution of defense and virulence in this tritrophic system, and we discuss the consequences of these insights for the "world is green" hypothesis and the common notion that plant–predator mutualisms readily evolve because "it is both in the interest of plants to get rid of the herbivores and in the interest of the predators to find herbivores as prey" (Price *et al.* 1980).

First, we briefly discuss that the players in the tritrophic game operate on very different spatial and temporal scales. Second, we introduce a simple model of local predator–prey dynamics on an individual plant based on specific scale assumptions and use this model to identify the main categories of defensive strategies of a plant, as well as the main strategies of food exploitation by the herbivores and the predators. Third, we identify evolutionarily stable strategies (ESSs) of exploitation (predator–herbivore, herbivore–plant), migration (predator, herbivore), and defense (plant, herbivore) in tritrophic systems. Finally, we speculate on the consequences for virulence management.

22.2 Spatial and Temporal Scales of Interaction

Plants, herbivorous, and predatory arthropods are engaged in interactions with widely different temporal scales. Plants usually have much longer generation times than arthropods. Hence, plant population change tends to be slow relative to that of the arthropods. Hence models of arthropod predator–prey dynamics are usually decoupled from plant population dynamics by assuming a pseudo-steady state. The generation times of herbivorous and predatory arthropods may also differ, but are usually close enough to justify modeling as a ditrophic system (Hassell 1978; Sabelis 1992).

The spatial scale of predator–prey interaction is set by the distribution of herbivorous arthropods. Many herbivorous arthropods have strongly clumped distributions over their host plants. This may be the result of:

- Aggregation toward weakened host plants or hosts whose defenses are overwhelmed by pioneer attacks, as in bark beetles (Berryman *et al.* 1985; de Jong and Sabelis 1988, 1989);
- Large egg clutches deposited by a female, as in various species of moths (larch bud moths, gypsy moths, ermine moths, tent caterpillars, and brown tail moths);
- Multigeneration congregations that result from one or a few founders with a high intrinsic capacity of population increase (relative to the rate of emigration) and low *per capita* food demands, as in many small herbivorous arthropods with short generation times (scale insects, mealybugs, aphids, leafhoppers, whiteflies, thrips, spider mites, and rust mites).

These groups of herbivorous arthropods may occupy a leaf area less than that of a plant, or cover several neighboring plants. Moreover, group size and the leaf area occupied increase with the number of generations spent in the group and with the

extent to which the herbivores move to neighboring host plants instead of dispersing far away. These traits are of crucial importance to understand plant defenses, because individual plants (or kin groups of plants) are the units of selection and the selective advantage of defense depends on the extent to which a plant can influence the local dynamics of herbivores and predators by direct and/or indirect defenses. Indeed, this influence is limited because predators and herbivores are independent players in the game: they may decide to stay, to move to neighboring plants, or to disperse far away. Hence the question is: does the defense of an individual plant initially affect the herbivore population it harbors (and much later the herbivore population as a whole) or does its impact on the herbivores permeate population-wide and without delay (as a consequence of high herbivore mobility)? Much the same questions can be formulated with respect to the degree in which individual plants can monopolize the advantages from attracting natural enemies of the herbivores. To analyze the complexities that arise from spatial and temporal scales we start by assuming that plants investing in direct and indirect defense acquire all the benefits, and later we consider the case in which neighboring plants may profit too.

22.3   Predator–Herbivore Dynamics on Individual Plants

To understand the range of possible plant defense strategies it is instructive to model the dynamics of small arthropod herbivores at the scale of an individual plant (or a coherent group of clonal plants). For reasons of simplicity we assume that the spatial scale covered by a local predator and prey population is smaller than that of an individual plant (or group of ramets) and that the individual plant does not impose a carrying capacity on the arthropod population that inhabits the plant. Moreover, we limit our discussion to the case of local populations with multiple and overlapping generations, as is realistic for small arthropods. Our aim is to find the simplest possible model for the dynamics of herbivorous and predatory arthropods and then ask the question how an individual plant can reduce damage by influencing the herbivores and their predators.

We assume that prey form patchy aggregations, which consist of clusters of herbivore-colonized leaves, and that predators entering such patches can freely move around, and spend little time in moving between herbivore-colonized leaves relative to the time spent within the herbivore colonies. Moreover, predators tend to avoid each other (Janssen *et al.* 1997a) and thereby interference (Nagelkerke and Sabelis 1998). Thus, the cluster of herbivore-colonized leaves can be considered as a coherent and homogeneous arena for strongly coupled predator–prey interactions (Figure 22.1). The population of herbivores in such a cluster presents to a predator in the same way as a host does to a pathogen. In fact, local predator–prey dynamics are much more transparent, and have been much more thoroughly studied, than within-host parasite dynamics. Usually, the latter are treated as a black box [but see Box 12.1 and, in addition, Nowak *et al.* (1991), Sasaki and Iwasa (1991), Antia and Koella (1994), for models that take within-host dynamics explicitly into
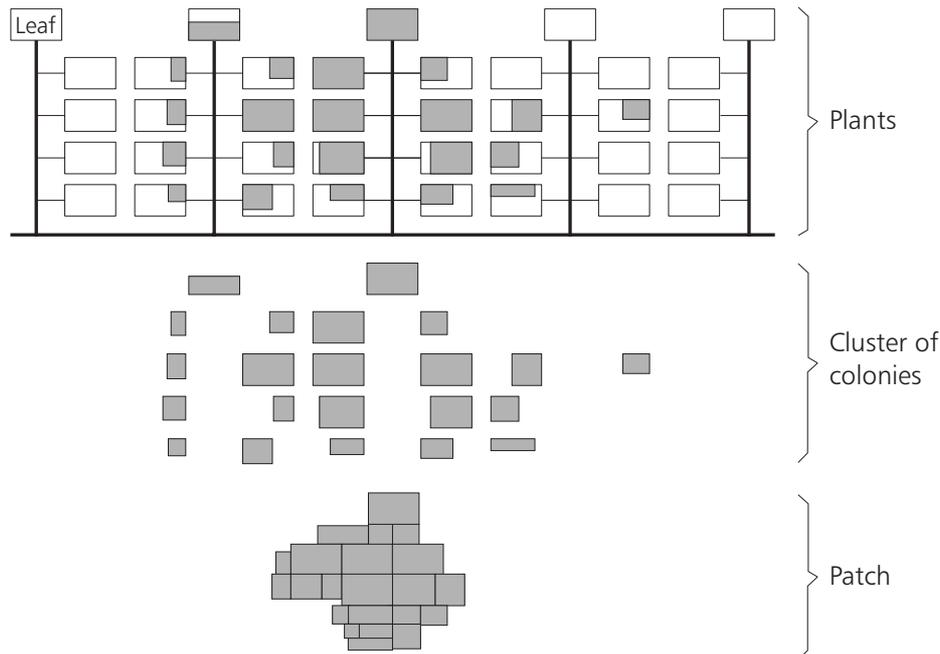
Figure 22.1 A patchy infestation of small herbivorous arthropods in a row of plants (side-view). It is inspired by observations on spider mites, but in essence applies to many other herbivorous arthropods. The infested leaf parts are excised (middle) and then put together as a jigsaw puzzle (bottom). The latter forms the patch or arena within which the interaction between predator and prey takes place (assuming negligible time spent in moving between infested leaves).

account], whereas various simple models capture the essence of local predator–prey dynamics.

To derive one example of such a model, we assume that the predators search for the highest prey densities and minimize interference with (intraspecific) competitors. In addition, we assume that within newly (and expanding) infested leaf areas herbivore density is typically constant, a characteristic determined by the herbivore or the combination of herbivore and plant (Sabelis 1990; Sabelis and Janssen 1994). Thus, per unit of plant area, herbivores raise a fixed amount of offspring and predators reaching a freshly colonized leaf site continue to eat prey until they do better by moving to a site nearby on the same plant. These assumptions lead to a constant rate of predation, which is much like "eating a pancake": a constant amount of food at each bite until there is nothing left.

As long as the pancake is not completely eaten, predators maximize the per capita rate of predation, development, and reproduction. Hence, under conditions of a stable age distribution they achieve their intrinsic rate of population increase. Similar assumptions are made with respect to herbivore growth capacity in the absence of the predators. For the case in which predators stay until all the prey are eaten, the dynamics of predator and herbivore numbers can be described by the two linear differential Equations (22.1a) and (22.1b). These differ from the classic Lotka–Volterra models in that the predation term now only depends on the number of predators (Metz and Diekmann 1986, example III.1.10; Janssen and
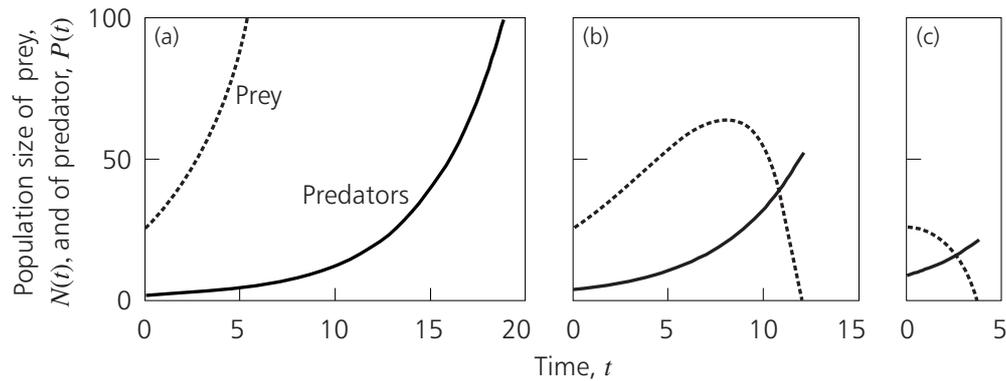
Figure 22.2 Three types of local predator–prey dynamics (continuous curve for predators and dashed curve for prey) according to the pancake predation model [with parameters $r_N = 0.3$, $k = 1$, $r_P = 0.25$, $m_P = 0$, and $N(0) = 25$]. (a) Prey increase, $P(0) = 1$, (b) delayed prey decline, $P(0) = 3$, and (c) immediate prey decline, $P(0) = 8$. The general conditions for each of these types of dynamics are discussed in the text.

Sabelis 1992; Sabelis 1992),

$$\frac{dN}{dt} = r_N N - kP \, , \tag{22.1a}$$

$$\frac{dP}{dt} = r_P P \, . \tag{22.1b}$$

This is the so-called "pancake predation" model with t = the time since start of the predator–prey interaction, $N(t)$ = number of prey at time t, $P(t)$ = number of predators at time t, r_N = rate of prey population growth, k = maximum predation rate, and r_P = rate of predator population growth. Analytical solutions for the number of predators and prey since the start of the interaction are readily obtained,

$$N(t) = N(0)e^{r_N t} - P(0)\frac{k}{r_P - r_N}(e^{r_P t} - e^{r_N t}) \, , \tag{22.2a}$$

$$P(t) = P(0)e^{r_P t} \, . \tag{22.2b}$$

Three types of dynamical behavior of the prey population may occur:

■ Continuous increase (but at a pace slower than the intrinsic rate of prey population growth; Figure 22.2a);
■ Initial increase, followed by decrease until extinction (Figure 22.2b);
■ Continuous decay until extinction (Figure 22.2c).

In the first case only, predatory arthropods cannot suppress local prey population outbreaks, but in the two other cases they eliminate the prey population and grow exponentially until a time τ when all the prey are eaten and all the predators emigrate. This time τ from predator invasion to prey extinction can be expressed as

a function of r_N, k and r_P and the initial numbers of predator and prey, $N(0)$ and $P(0)$,

$$\tau = \frac{1}{r_P - r_N} \ln \left[1 + \frac{r_P - r_N}{k} \frac{N(0)}{P(0)} \right] . \tag{22.3}$$

Immediate decline of the herbivores occurs when the net growth rate of the herbivore population is negative, $r_N N(0) < k P(0)$, or

$$\frac{P(0)}{N(0)} > \frac{r_N}{k} . \tag{22.4a}$$

Thus, for the herbivore population to decline immediately, the ratio of predators to herbivores should exceed the ratio of the per capita population growth rate of the herbivore and the maximum per capita predation rate.

The conditions for continued herbivore increase are found by calculating the condition for which the time to prey extinction has a finite value. Provided that the plant is not overexploited during predator–prey interaction, this condition is

$$\frac{P(0)}{N(0)} \leq \frac{r_N - r_P}{k} . \tag{22.4b}$$

This condition cannot hold when the growth rate of the prey does not exceed that of the predator, $r_N \leq r_P$. Whenever the condition is met, however, herbivores continue to increase and predators "surf" on the "population growth wave" of the herbivore. Inevitably, this increase stops when the plant becomes overexploited.

The total damage incurred by the plant over the whole interaction period can be expressed in the number of herbivore-days D, that is, the area under the curve that expresses the temporal changes in the size of the herbivore population,

$$D(\tau, r_N, k, r_P, N(0), P(0)) = \frac{1}{r_N} \left[P(0) \frac{k}{r_P} (e^{r_P \tau} - 1) - N(0) \right] . \tag{22.5}$$

Note that this measure of the damage strongly depends on the exponential term and thus on the time to prey extinction τ and the per capita growth rate of the predator population r_P.

Thus, given the initial population sizes $N(0)$ and $P(0)$ and estimates of the parameters r_N, k, r_P, it is possible to assess the overall damage by the herbivore and the predator's potential to suppress the prey population immediately, with a delay, or not at all. Now, we may ask how a plant can influence the local dynamics so as to minimize herbivore damage. Under the assumption that the parameters can be modified independently, the answer is straightforward. It should:

- Make the predator-to-herbivore ratio as high as possible;
- Increase the predation rate or the predator growth rate;
- Decrease the growth rate of the herbivore.

To illustrate this, the plant may attract and retain the predators by providing SOS signals upon herbivore attack, it may provide food and shelter for the predators, and produce toxins or digestion inhibitors.
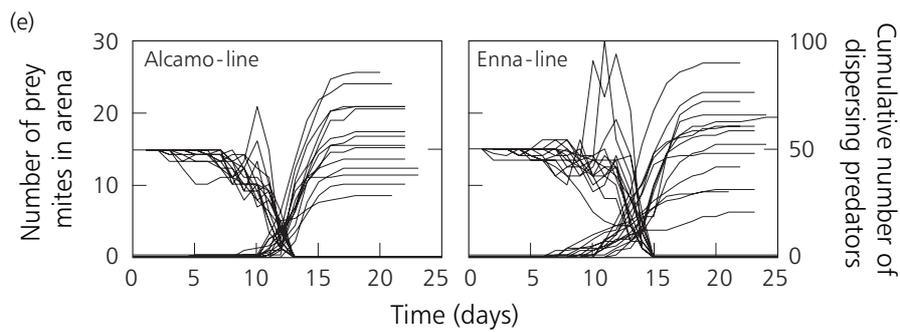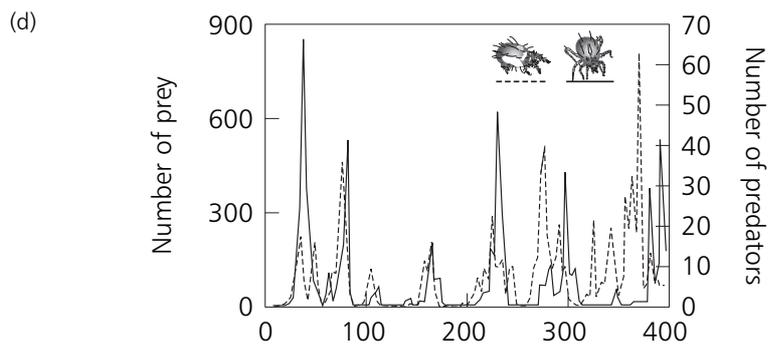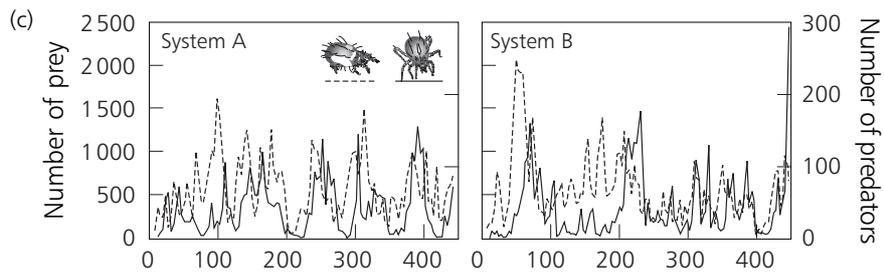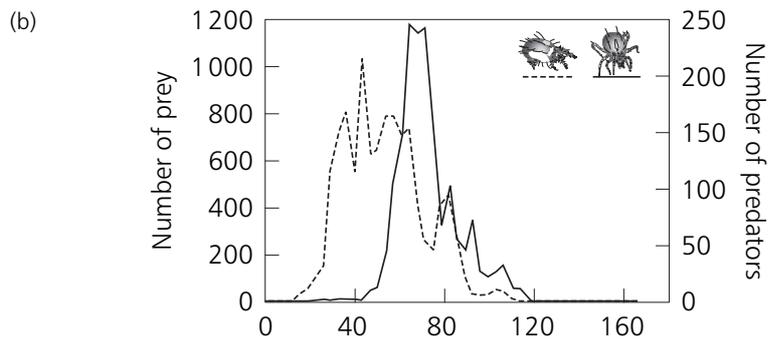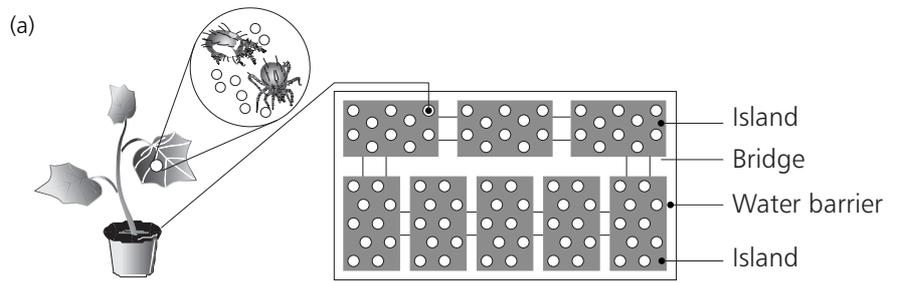
Figure 22.3 Dynamics of predatory mites (*Phytoseiulus persimilis* Athias-Henriot; continuous curves) and herbivorous mites (*Tetranychus urticae* Koch; dashed curves) at various spatial scales. (a) Circular system of eight interconnected islands (trays), each with 10 Lima-bean plants maintained in the two-leaf stage (by frequent removal of the apex and replacement of plants exhausted as a food source). *Source*: Janssen *et al.* (1997b). (b) Extinction-prone predator–prey dynamics on one super-island (the size of eight trays together). (c) Two replicate experiments showing persistent predator–prey metapopulation dynamics on the eight-island system in (a). (d) Extinction-prone predator–prey dynamics on one of the trays shown in (a). *Source*: Janssen *et al.* (1997b); see also Van de Klashorst *et al.* (1992). (e, left) Extinction-prone predator–prey dynamics on a single leaf in a wind tunnel, using a field-collected predator line selected for nondispersal before prey extermination. *Source*: Pels and Sabelis (1999); see also Sabelis and Van der Meer (1986). (e, right) As (e, left), but now using a field-collected predator line selected for dispersal before prey extermination. *Source*: Pels and Sabelis (1999).

Trade-off relations between parameters may complicate matters. For example, decreasing the growth rate of the herbivore r_N by toxins may also intoxicate the predator, thereby decreasing the predation rate k and/or its growth rate r_P. In the extreme, the herbivore may even use the plant-provided toxins to defend itself against predators. Thus, the plant does not always profit from decreasing the growth rate of the herbivore. It only profits if it decreases the herbivore's growth rate proportionally stronger than the predation rate and the growth rate of the predator.

Another message gleaned from the equations is that plants may benefit from promoting the presence of predators with high predation rates and high growth rates. Often, these demands are in conflict with each other, because the predation rate tends to increase with body size, whereas the intrinsic rate of population increase tends to decrease with body size (Sabelis 1992). Such relationships with body size are clear from analyzing published data on predators of phytophagous thrips, such as mirids, anthocorids, predatory thrips, and predatory mites (Sabelis and Van Rijn 1997). At lower taxonomic levels (within family, within genus) the picture may be different. For example, within the *Phytoseiidae* – a family of plant-inhabiting predatory mites – positive high correlations between k and r_P exist (Janssen and Sabelis 1992; Sabelis and Janssen 1994). It may be possible that the plant could selectively attract one species of predator over the other and thereby profit from selecting the more effective predators. However, how a plant could do so, given that predators will seek the most profitable prey, remains to be shown.

Predators are independent players in the tritrophic game and they decide whether it is profitable to stay on a plant or not. The pancake predation model is based on the assumption that predators are strongly retained and stay until all the prey are eaten. This scenario is not implausible, because it may be risky to disperse and search for new herbivore patches. Indeed, it is frequently observed, as in interactions among predatory mites and spider mites (Figure 22.3a; Sabelis and Van der Meer 1986). One may, of course, expect predators to leave somewhat earlier than the exact moment of prey extinction. This would relieve the herbivores from
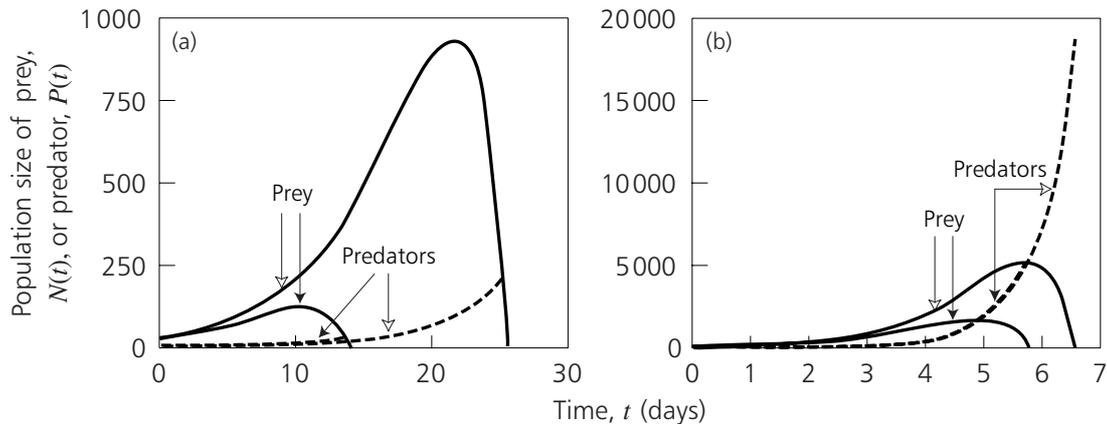
Figure 22.4 Influence of emigration on local predator–prey dynamics according to the pancake model. (a) Predator emigration rate m_P equals zero for predator and prey curves indicated by filled arrowheads, whereas it is 0.04 for the predator and prey curves indicated by open arrowheads. Parameters: $m_P = 0$ or 0.04, $r_N = 0.3$, $k = 3$, $r_P = 0.25$, $N(0) = 30$, $P(0) = 1$. (b) Prey emigration rate m_N equals zero for dashed predator and prey curves (open arrowheads) and 0.1 for the continuous predator and prey curves (filled arrowheads). Parameters: $m_N = 0$ or 0.1, $r_N = 1$, $k = 1$, $r_P = 1.5$, $N(0) = 50$, $P(0) = 1$.

predation pressure and predator-to-prey ratios may become so low that the herbivore population increases again, thereby giving rise to cyclic dynamics. The plant would then accumulate damage over the predator–prey cycles whereas it would be better off when predators exterminate the herbivores or maintain them at a very low level. Examples of local predator–prey dynamics are shown in Figure 22.3 for interactions between phytoseiid predators and spider mites. Similar examples are known from interactions between phytoseiid mites and thrips, and anthocorid predators and thrips (Sabelis and Van Rijn 1997). All these examples convincingly show that local herbivore populations are strongly suppressed by predators. Thus, the dynamics of the "pancake predator" model seems to be a good caricature of the initial predator–prey population cycle. Thus, for all cases in which one cycle of predator and prey colonization occurs before extermination, this model is useful to understand the role of indirect and direct defenses of a plant.

Predator retention during the interaction with the herbivores is decisive in the success of indirect defense strategies of the plant. For example, if we extend the pancake predator model with a constant predator emigration rate (i.e., independent of prey availability), then emigration acts to decrease the effective population growth rate of the predators. As shown in Figure 22.4a small decreases of the population growth rate have dramatic consequences for the duration of the interaction and even more for the number of herbivores attacking the plant. The overall damage to the plant increases nonlinearly with a reduction of the predator's population growth rate. Hence, it is important to observe that several species of predators are strongly retained in herbivore-colonized patches and tend not to leave until the prey population is near extinction (Sabelis and Van der Meer 1986; Sabelis and Van Rijn 1997; Pels and Sabelis 1999; Figure 22.3e).

The herbivore can always make the last move in the tritrophic game. Not only may they develop resistance against the predators and overcome barriers raised by the plant, but ultimately, they may also decide to leave the plant. If the plant drives herbivores away by attracting predators, and also by stimulating herbivore emigration, then it benefits disproportionately, as illustrated in Figure 22.4b.

In conclusion, there are various ways in which a plant can benefit by influencing behavior and dynamics of predators and herbivores. Direct plant defenses do not merely slow down the herbivore's growth rate, they may also affect predator impact, either positively (higher predator-to-herbivore ratio) or negatively (plant toxins protecting herbivores against predators). Indirect defenses do not merely affect predator performance, they may also affect selection on herbivores, be it positive (enemy avoidance) or negative (resistance to predators) for the plant. Hence, to understand the plant's allocation to direct and indirect defenses we should not only assess the costs, but also elucidate how these two types of defenses interact in their impact on overall herbivore damage.

22.4 Tritrophic Game Theory and Metapopulation Dynamics

The evolution of direct and indirect plant defenses against arthropod herbivores is by no means a simple process. For one thing, we have to take the defense and exploitation strategies of all three trophic levels into account. For another, time scale and spatial scale arguments force us to consider metapopulation models with the full tritrophic structure, and – as we emphasize later – to incorporate plant dynamics adds new dynamical behavior to the repertoire of the otherwise ditrophic models.

Indeed, evolution in structured populations can only be properly understood by taking metapopulation structure into account. The strategies play against each other at the patch level and their relative success determines metapopulation dynamics. In turn, metapopulation processes determine which strategies will meet and compete again at the patch level. This chain of processes is referred to herein as the ecological feedback.

To gain insight into this complex problem, carefully planned simplifications are required. Our strategy is first to consider the evolution of relevant traits at one trophic level in pairwise interactions with one other level (predator–herbivore; herbivore–predator; plant–herbivore; herbivore–plant; plant–predator; predator–plant), thereby assuming a steady state at the metapopulation level. We conclude with a tentative, verbal discussion of what may happen evolutionarily in the full tritrophic system.

The predator's dilemma: to milk or to kill?

It is one thing for a plant to attract and retain predators, but it is another to lure predators that also effectively suppress the herbivore population on the plant. Clearly, it is the predator who reacts to the lure, and decides how fast it will consume herbivores, how fast it will multiply, and how long it will stay. In

other words, the effectiveness of indirect plant defenses depends on the herbivore-exploitation strategies present in the predator population. In principle, these exploitation strategies can be many and varied. To illustrate this point it is instructive to use the "pancake" model to examine local predator–herbivore dynamics. The strategy set is determined by combinations of the per capita growth rate of the predator r_P and the per capita predation rate k. However, a spatially structured environment has one more parameter: the per capita emigration rate of the predator. Of course, all predators disperse away when herbivores are exterminated and there is no other food, but they can also decide to move away during the interaction. Such increased emigration of the predator relieves the prey of predation pressure and thereby the prey population represents a larger future food source for the predator (Van Baalen and Sabelis 1995c). This effect can also be achieved by decreased predation (Gilpin 1975). However, increased emigration during the interaction seems a more sensible strategy, because it does not affect the intrinsic population growth rate, whereas decreased predation implies lower food intake and thereby a lower population growth rate. Moreover, the extra dispersing propagules generated under the former strategy will promote the founding of new populations. In what follows we therefore focus on the predator's migration trait alone.

Let us assume for simplicity that the per capita emigration rate is a constant m_P. The effective per capita population growth rate of the predators is reduced by m_P so that the effective predator growth rate now equals

$$\frac{dP}{dt} = (r_P - m_P)P \; . \tag{22.6}$$

As decreased values of r_P have been shown to drastically alter local predator–prey dynamics, so do increased values of m_P. As illustrated in Figure 22.4a, a small increase of m_P from 0 to 0.04 day^{-1} greatly alters the area under the prey curve and thereby also the damage to the plant. Hence, a plant benefits from stimulating predators to stay until all the prey are eliminated, but whether it succeeds depends on what is best for the predators (as well as on the ecological feedback). The local success of a predator's exploitation strategy may be expressed as the number of dispersers produced during the interaction with prey, plus those that disperse after prey extermination. As shown in Figure 22.5, the production of dispersers increases disproportionally with m_P and reaches an asymptote when the per capita emigration rate is so high that the predators cannot suppress the growth of the prey population any more, that is, when $m_P = r_P - r_N + kP(0)/N(0)$. Thus, predators that suppress emigration during the interaction reach their full capacity to suppress the local prey population, but they produce the lowest number of dispersers per prey patch. In terms of production of dispersers this so-called *killer* strategy does less well than the strategy of a *milker*, which typically has a nonvanishing emigration rate during the predator–prey interaction period. However, if killers enter a prey patch with milkers, then they would steal much of the prey the milkers had set aside for future use. Therefore, if there is a risk of invasions by killers, it pays to anticipate such events and selection will favor exploitation strategies that are less milker-type and more killer-type.
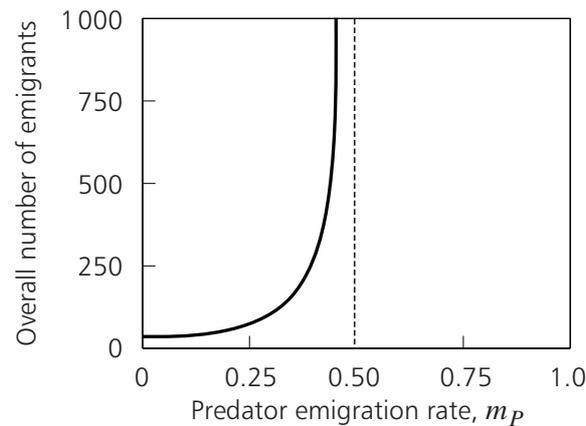
Figure 22.5 The relation between the overall production of predator dispersers and the per capita rate of emigration m_P during the predator–prey interaction period (from predator invasion to prey elimination. *Source*: Van Baalen and Sabelis (1995c).

The outcome of the milker–killer dilemma is determined by a complex interplay of local competition between the exploitation strategies and global (= metapopulation) dynamics. It depends on the probability of multiple predator invasions in the same prey patches (or, alternatively, on the probability of exploiting a prey patch alone), on the resultant production of dispersers per prey patch, and on metapopulation dynamics, as this in turn determines the probability of multiple invasions. The complexity of this ecological feedback is staggering; to keep track of the numbers of each strategy type when competing in local populations, dispersing into the global population, and invading into local populations requires a massive bookkeeping procedure. Hence, we are bound to simplify to obtain some insight. For example, Van Baalen and Sabelis (1995c) assumed that all patches start with exactly the same number of predators and prey (which assumes metapopulation-wide equilibrium and ignores stochastic variation in the number of colonizers) and that the predators have enough time to reach their full production potential per prey patch (the assumption of sequential interaction rounds). In this setting they considered the reproduction success of one mutant predator clone with a per capita emigration rate, $m_{P,\text{mut}}$, relative to the mean success of predators in the population of the resident clone, which possesses another per capita rate of emigration, $m_{P,\text{res}}$. The question is whether there exists an ESS value of $m_{P,\text{res}}$ for which it does not pay any mutant to deviate (Maynard Smith 1982). In particular, Van Baalen and Sabelis (1995c) calculated the combinations of parameters $P(0)$, $N(0)$, r_N, k, and r_P for which it does not pay to increase m_P away from zero, that is, the conditions that favor selection for killers. As illustrated in Figure 22.6, the general outcome is that killers are usually favored by selection, except when the number of predator foundresses is low and the number of prey foundresses is high. In other words, the milkers are favored as long as they have a sufficiently large share in the local populations to maintain control over the time to prey elimination τ.

This analysis whets the appetite for more elaborate considerations that account for:
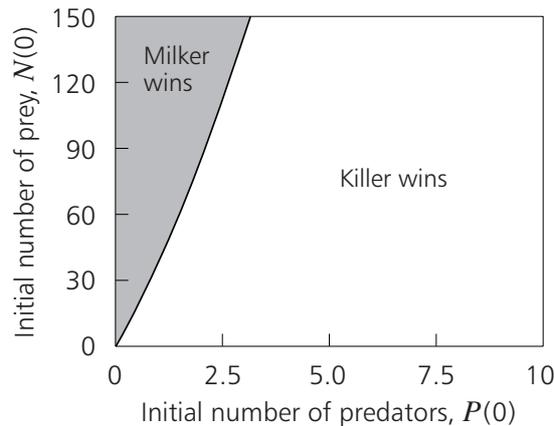
Figure 22.6 When does it pay to increase the per capita emigration rate of the predator m_P away from zero? This diagram shows that milker strategies are only advantageous when $P(0)$ is low and $N(0)$ sufficiently high. *Source*: Van Baalen and Sabelis (1995c).

- Asynchrony in local dynamics;
- Stochastic variation in predator and prey colonization rates (since these are probably low);
- An upper boundary to prey population size set by the local amount of food;
- Metapopulation dynamics.

Such extensions are likely to show that milkers which achieve a longer interaction period are also exposed for a longer period to subsequent predator invasions (and thus face competition with killers sooner or later), that stochastic rather than uniform invasions help to isolate milkers, which thereby gain full advantage of their exploitation strategy, and that limits to the amount of food available for the prey decrease opportunities for a milker, as it loses full control over the interaction period τ. As these factors have opposite effects it is not immediately clear whether killers or milkers will win the battle or whether they may even coexist. Computer simulations of the metapopulation dynamics of milkers and killers using a model parameterized for phytoseiid mites (predators) and spider mites (prey; Pels *et al.*, in press) showed that the full ecological feedback gives rise to prey and predator densities in which multiple predator invasions are sufficiently rare to make "milkers" the more successful strategy. The results of a large number of computer experiments to determine the average number of dispersers born from mutants with different emigration strategies released randomly in the metapopulation of the residents (but after 2 000 days to avoid the initial phase of transient metapopulation dynamics) is summarized in the pairwise invasibility plot shown in Figure 22.7. This shows that metapopulation dynamics can force the predator–prey system into a state [i.e., number of predator and prey colonizing a patch, $N(0)$ and $P(0)$, in Figure 22.6] in which "milkers" are the winners of the competition.

Apart from the need for more theoretical work, experimental analysis of variation in the exploitation strategies of predators seems a promising avenue for future research. Such an analysis, carried out for the predatory mite *Phytoseiulus persimilis* Athias-Henriot, revealed that laboratory cultures harbor exclusively predators
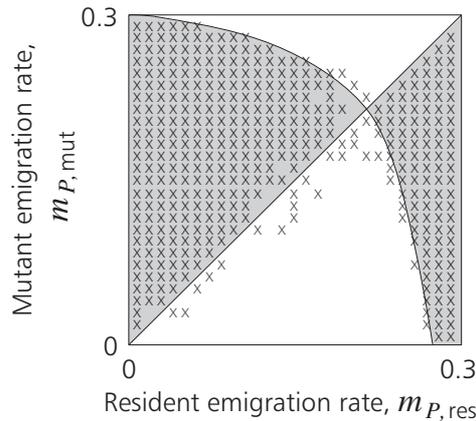
Figure 22.7 A pairwise invasibility plot for mutants that differ from the resident predators with respect to the emigration rate m_P. The resident's emigration rate is given on the horizontal axis and the mutant's emigration rate on the vertical axis. Gray areas indicate combinations in which the mutant invades the resident population (the shape of the gray areas is based on the simulation results indicated by crosses). The results shown are obtained for a value of the predator's survival rate that allows the predator–prey system to persist.

of the killer type (Sabelis and Van der Meer 1986), whereas field-collected populations in the Mediterranean (Sicily) exhibit some variation in the onset of emigration before or after prey elimination (Pels and Sabelis 1999). Interestingly, most populations collected along the coast, where predators are more abundant, initiated emigration only after elimination of the prey, whereas those collected inland, where local predator populations are scarce and hence more isolated, showed some emigration before prey elimination! These results are in qualitative agreement with the analytic ESS analysis of Van Baalen and Sabelis (1995c; Figure 22.6), but they seem to contradict the results of the more "realistic" computer simulations that are not only parameterized for this particular mite system but also take into account stochastic colonization and the full ecological feedback (Pels *et al.*, in press; Figure 22.7). This discrepancy probably results from a variety of factors that cause the predators to loose control over the exploitation of the local prey population. Examples are environmental disasters (heavy rain, wind, or fire), overexploitation of plants by large herbivores, and also exploitation competition with other predator species or herbivore diseases. The discrepancy between the simulations (Pels *et al.*, in press; Figure 22.7) and the analytic treatment (Van Baalen and Sabelis 1995c; Figure 22.6) may emerge because:

■ The simulations were obviously only carried out for persisting resident populations, whereas the analytic treatment implicitly assumed equilibrium (and thus persistence);

■ The simulated predator–prey feedback causes patches to be invaded by very low numbers of predators, whereas the analytic treatment presupposed a certain invasion scenario (equal for all patches);

■ The stochastic colonization process of the predators allows some patches to be invaded singly and gives the single invader full control over the exploitation

of the local prey population, whereas the analytic treatment ignored stochastic variation in the number of colonizers.

Obviously, the prevalence of killers is of great importance for the evolution of indirect plant defenses. By providing protection and food to predatory arthropods and by signaling herbivore attack to predators, plants increase the predator invasion rate into young colonies of the herbivorous arthropods. This promotes the probability of coinvasions of milkers and killers, which – other things being equal – ultimately favors the latter. Yet, there may be a pitfall in that, so far, neither theoretical nor experimental analyses addressed the possibility of more flexible strategies, such as: "milk when exploiting the prey patch alone, and kill when other (e.g., nonkin) predators have entered the same patch."

In summary, how "virulent" predators should be (as "parasites" of local herbivore populations) depends on whether they are able to monopolize this resource. Sharing of the resource with other clones ("multiple infection") favors increased virulence. How often such sharing occurs depends on the ecological feedback loop. To a certain extent, this conclusion is more robust than those based on other models published in the epidemiological framework (e.g., Nowak and May 1994; Van Baalen and Sabelis 1995a), because it is based on an explicit consideration of how the predator's exploitation strategies affect the interaction time in the patch (and not on some *a priori* assumption about the relation between parasite transmission and host mortality).

The herbivore's dilemma: to stay or to leave?

Just like the predators, the herbivores are independent players in the tritrophic game. When their local populations are discovered and invaded by predators of the milker type, possibilities to achieve reproduction success remain, especially if the milker has such a high emigration rate that it cannot suppress the herbivore population. However, when killers enter the herbivore population, it may pay the herbivores to invest in defense against the killer-like predators or to leave the prey patch in search for enemy-free space. For simplicity, we consider the last type of response only. Consider the pancake predation model again, but now extended with a per capita emigration rate m_N of the herbivore:

$$\frac{dN}{dt} = (r_N - m_N)N - kP \ , \tag{22.7a}$$

$$\frac{dP}{dt} = r_P P \ . \tag{22.7b}$$

As shown in Figure 22.4b, an increase in m_N causes the time to prey elimination to decrease, as will the overall, local herbivore population (i.e., the area under the herbivore population curve) and the number of predators that will disperse. We may now ask whether there is an evolutionarily stable (ES) emigration rate. To obtain an answer we should first define reproduction success as the per capita emigration rate m_N multiplied by the area A under the herbivore curve (which

itself depends on m_N), divided by the initial number of herbivores $N(0)$. This fitness measure always shows a maximum for intermediate values of m_N, because A decreases rapidly with m_N. Suppose, for simplicity, that all patches start synchronously with the same initial number of predators and herbivores and that each patch is colonized by $N(0)$ herbivore clones with $m_{N,\text{res}}$ and just one herbivore mutant clone with $m_{N,\text{mut}}$. Further, assume that the two types of herbivore clones are attacked in proportion to their relative abundance, but that the mutant is so rare that $N_{\text{res}} + N_{\text{mut}} \approx N_{\text{res}}$. This makes herbivore dynamics in the patch and time to prey elimination τ entirely dependent on the resident population. The mutant's presence does not influence the growth of the resident herbivore population and neither does it affect the growth of the predators. Herbivore dynamics in the patch and time to prey elimination τ are thus entirely dependent on the traits of the resident prey population. Now, we ask whether there is a resident herbivore population with $m_{N,\text{res}}$ that cannot be invaded by a mutant with another value of $m_{N,\text{mut}}$. The results presented in Figure 22.8 (Egas *et al.*, unpublished; for model details see Appendix 22.A) show that the ES emigration rate m_N^* increases with:

- Decreasing per capita population growth rate of the herbivores r_N;
- Increasing per capita predation rate k;
- Increasing per capita population growth rate of the predators r_P, and, thus, with a decrease in time to prey elimination τ.

Moreover, the larger the initial number of herbivores, the longer the time to prey elimination and the smaller the ES emigration rate m_N^*.

These results provide some important clues as to how the ES emigration rate m_N^* will change with the exploitation strategy of the predators. This is because predator emigration affects the effective predator growth rate as experienced by the prey. Milkers are predators with an effectively lower per capita rate of population growth, $r_P - m_P$, because of nonvanishing emigration, and the lower the predator's population growth rate, the lower the ES emigration rate m_N^* of the herbivore will be. Thus, a prevalence of milkers in the predator population causes selection for lower emigration rates of the herbivores (i.e., an increased tendency to stay in the herbivore aggregation), whereas a prevalence of killers causes selection for higher herbivore emigration rates. The ES emigration rate m_N^* appears to be always intermediate between 0 and r_N. Thus, herbivores may still aggregate in the face of killer-like predators.

Much remains to be learned as to how the evolution of plant defense strategies interferes with that of herbivore emigration. Increased efforts in direct plant defense probably decrease the per capita rate of herbivore population growth r_N, and as a by-product this triggers selection for a higher ES emigration rate of the herbivores m_N^*. Thus, ultimately the effective per capita rate of herbivore population growth, $r_N - m_N^*$, decreases even more. This paves the way for the evolution of feeding deterrents. The same applies to increased investments in indirect plant defenses. When plants promote the per capita predation rate k or the per capita
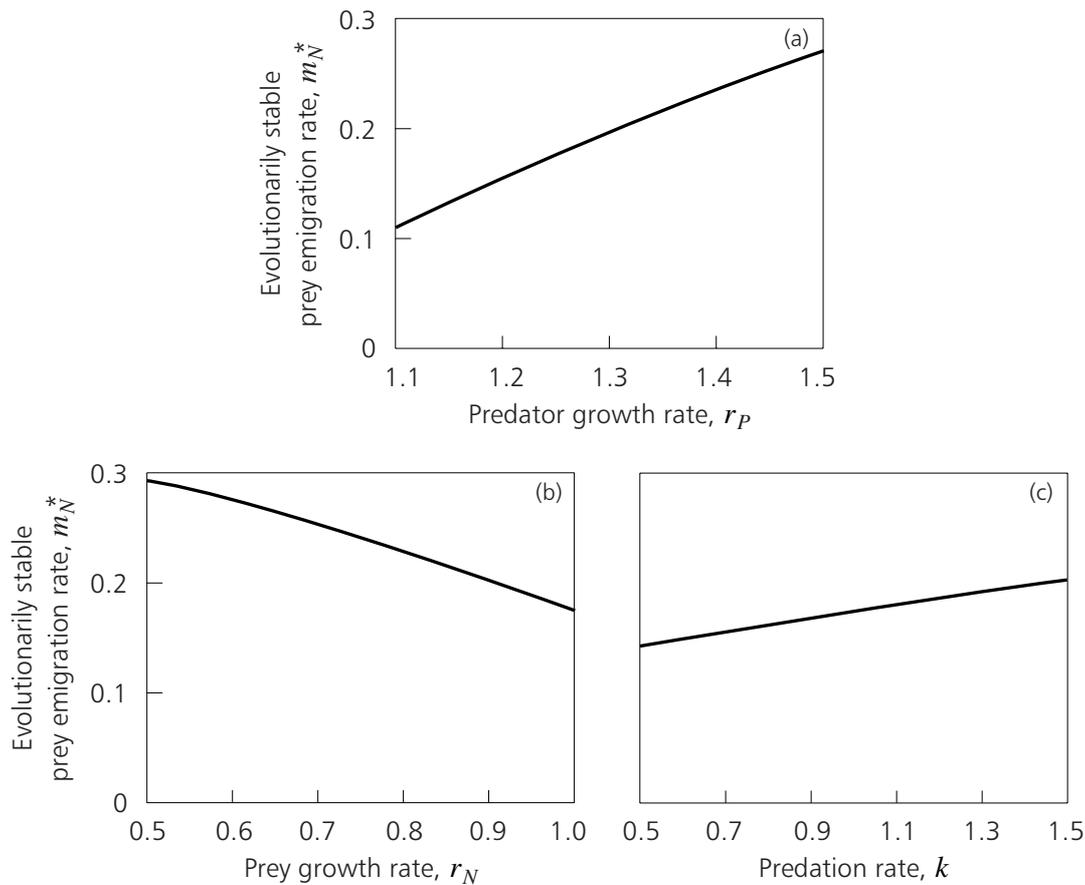
Figure 22.8 ES patch-emigration rates of prey in a predator–prey metapopulation. (a) The ES prey emigration rate m_N^* as a function of predator growth rate r_P. (b) Relation between ES emigration rate m_N^* and the prey growth rate r_N. (c) Relation between ES emigration rate m_N^* and the prey consumption rate k. Default parameter values: $N_{\text{res}}(0) = 49$ (a) or 99 (b, c), $N_{\text{mut}}(0) = 1$, $P(0) = 1$, $r_N = 1$, $r_P = 1.5$, $k = 1$. *Source*: Egas *et al.* (unpublished).

rate of predator population growth r_P, the by-product is that selection favors increased ES emigration rates of the herbivores, thereby lowering the effective rate of herbivore population growth, $r_N - m_N^*$. Thus, plants may also invest in releasing herbivore deterrents, signaling a high risk of being eaten by predators, and the herbivores are selected for vigilance in detecting the actual presence of predators. There are several examples of herbivorous arthropods that prefer plants with a lower risk of falling victim to natural enemies, despite their lower food quality (Fox and Eisenbach 1992; Ohsaki and Sato 1994). However, it is still unclear why the low quality plants are visited less frequently by the natural enemies of the herbivores. Another speculative, but potentially nice, illustration of plants signaling their predator-defended state to herbivores is found in the work of Bernasconi *et al.* (1998). When corn leaf aphids feed upon them, maize plants respond by releasing a blend of volatile compounds that repels other corn leaf aphids in search for hosts and also attracts parasitoids and lacewings. Interestingly, the blend of plant volatiles contains a monoterpene, (E)-β-farnesene, that corresponds to the alarm

signal released by the corn leaf aphid upon predator attack. Another potential example of plants signaling predation risk is given by Pallini *et al.* (1997), who found that spider mites prefer odor from spider-mite infested cucumber plants over odor from thrip-infested cucumber plants, whereas the thrips show no preference. Both spider mites and thrips are herbivores, but the thrips can also act as a predator of spider-mite eggs. Thus, the olfactory avoidance-response of the spider mites may be to avoid competition as well as predation risk. Recently, Pallini *et al.* (1999) found more evidence for the avoidance of predation risk in spider mites. They demonstrated that spider mites prefer odor from plants with spider mites alone over odor from plants with spider mites and the predatory mite *P. persimilis*. Possibly, the odor signal comes from conspecific spider mites that had direct contact with the predators, but this remains to be shown.

The plant's dilemma: direct, indirect, or no defense?

By investing in direct and indirect defenses, a plant gains protection against herbivory, but in doing so it also benefits its neighbors. If these are close kin, an individual plant also increases its inclusive fitness by investment in defense; but if not, it may well promote the fitness of its competitors for the same space and nutrient sources. Thus, the neighbor gains associational protection (Atsatt and O'Dowd 1976; Hay 1986; Pfister and Hay 1988; Fritz and Nobel 1990; Fritz 1995; Hjältén and Price 1997). This leads to the plant's dilemma: should it defend itself, thereby benefiting its neighbors as well, or decrease its defensive efforts? The solution is simple: the defenses should protect the plant without benefiting palatable neighbors too much. When its neighbors are well defended, a plant can afford to invest less itself.

When plants are (constrained to be) either undefended or well defended and herbivores do not discriminate between them, three outcomes are possible:

■ All plants are palatable;
■ All plants are well defended;
■ There is a stable mixture of palatable and well-defended plants.

Coexistence of the two types is possible when either of them increases when rare; in a population of well-defended plants a rare palatable plant can easily gain cheap protection by associating closely with a well-defended plant, whereas in a population of palatable plants a rare, well-defended plant does better as it benefits only few of the palatable individuals and, hence, increases the average fitness of the palatable plants only very little. When either of the two types gradually increases its share in the total population, the benefits wane and ultimately balance the costs, thereby giving rise to a polymorphic plant population (Sabelis and de Jong 1988; Augner *et al.* 1991; Tuomi and Augner 1993; Augner 1994).

The conditions for polymorphism are quite broad, but some of the critical assumptions are not generally valid. For example, herbivores are likely to distinguish between palatable and well-defended plants. In that case, an individual plant is likely to benefit from direct defenses and may even drive the selective herbivores
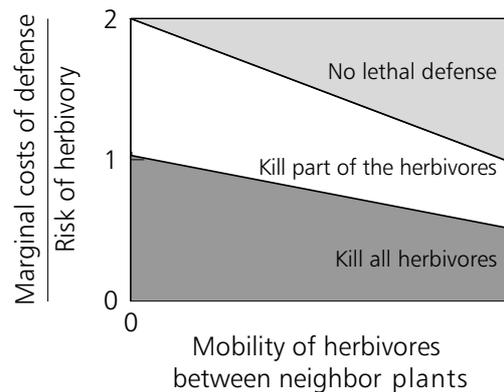
Figure 22.9 The effect of herbivore mobility (horizontal axis) on the parameter areas in which the ESS is to kill the herbivore (dark gray region), to kill part of the herbivores (intermediate, white region), and not to invest in killing herbivores at all (light gray region). The extent of these areas depends on the ratio of marginal costs of plant defense and the initial risk of herbivory. The cost of herbivory equals one if the herbivore survives, and 0.5 if it dies. *Source*: Tuomi *et al.* (1994).

toward the palatable plants. It should be noted that this mechanism does not apply to indirect defenses. Predatory arthropods are usually more mobile than the prey (stages) they attack and they readily move from the plant that employs them as bodyguards to a neighbor plant when the latter is under herbivore attack. Thus, even when the herbivore is a selective feeder, palatable plants profit more easily by settling close to a plant defended by predatory arthropods as bodyguards. Clearly, this mechanism promotes polymorphism (Sabelis and de Jong 1988). However, when defensive plant strategies are not discrete, but continuous (i.e., they cover the full range of possible investment levels), then there may be no polymorphism because ultimately all the plants will exhibit the best average defensive response.

The latter case was analyzed by Tuomi *et al.* (1994). They assumed that the cost of defense increases linearly with the probability of killing the herbivore, the slope being referred to as the marginal cost of defense (i.e., how fast costs increase with the impact of defense on the herbivore). The ES lethality level depends on the risk of herbivory, the marginal cost of defense, and the mobility of the herbivores between neighbor plants, as shown in Figure 22.9. When herbivory risks are low and marginal costs of defense high, then it does not pay to kill the herbivore. However, when the risk of herbivore damage is high and marginal defense costs are sufficiently low, then it pays to kill the herbivore. For intermediate ratios of marginal defense costs and risk of herbivory, ES lethality depends on the mobility of the herbivore between neighboring plants (Tuomi *et al.* 1994). Obviously, high mobility causes neighboring plants to share the same herbivores and selects for lower lethality levels, whereas low mobility selects for increased lethality. It is becoming increasingly clear that neighboring plants may communicate via damage-related signals (Farmer and Ryan 1990; Bruin *et al.* 1992, 1995; Shonle and Bergelson 1995; Adviushko *et al.* 1997; Shulaev *et al.* 1997), so it may well

be that plant defenses include strategies conditional upon the neighbor's state, as defined by:

■ Whether it is actually under attack;
■ Its defensive response.

This is a largely open problem in need of further theoretical and experimental work.

Whether the effects of defensive efforts occur in discrete jumps or are more gradual is an important determinant of the existence of polymorphism, but the most relevant message is that in both cases associational protection may lead to a lower average investment in defenses. This applies to direct defenses (Tuomi *et al.* 1994), as well as to indirect defenses (Sabelis and de Jong 1988).

But coevolution may act as a boomerang ...

The most elusive unknown of all is the interplay between metapopulation dynamics and evolution at all three trophic levels. To assume a steady state metapopulation is clearly an oversimplification in view of the complex dynamics (e.g., bistability, chaos) that may arise by adding an extra trophic level to ditrophic models (Sabelis *et al.* 1991; Jansen and Sabelis 1992, 1995; Klebanoff and Hastings 1994; Jansen 1995; Kuznetsov and Rinaldi 1996) or the complexities that may arise from the interactions within food webs of arthropods on plants (intraguild predation; "prey-eats-predator"; apparent competition; Holt 1977; Polis *et al.* 1989; Polis and Holt 1992; Holt and Polis 1997). Thus, where the tritrophic system will settle evolutionarily is very hard to predict.

To illustrate this, it is worthwhile to carry out an – admittedly speculative – thought experiment. Consider what will happen when plants evolve to invest more in direct and indirect defenses, and predators are initially of the killer type. First and foremost, increased defensive efforts by the plant decrease the size of the herbivore's metapopulation. Subsequently, the size of the predator's metapopulation decreases which in turn causes a drop in the rate of predator invasion into herbivore patches. As a consequence, the probability of coinvasion of predators with different prey-exploitation strategies into the same herbivore patch decreases, thereby providing a selective advantage to predators that are more milker-like. In addition, increased plant defense promotes herbivore emigration and decreases the size of local herbivore populations. This also decreases the probability of predator coinvasion and thus selects for milkers. Thus, the plant's investment in defense may ultimately result in ineffective predators; this we call boomerang coevolution. It is typically the consequence of adding one more trophic level to an exploiter–victim system and allowing strategies of exploitation and defense to vary at each trophic level.

A similar thought experiment can be carried out for the case that not only does the plant benefit from its own investment in direct and indirect defenses, but so do its neighbors, who may well be competitors (Sabelis and de Jong 1988; Augner *et al.* 1991; Tuomi *et al.* 1994). Again, increased investment in plant defense

causes a boomerang effect because neighboring plants profit and allocate the energy saved directly to increase their seed output or indirectly by increasing their competitive ability.

Boomerang coevolution arises through the impact of plant defenses on alternative allocation strategies of neighboring plants and via the positive effect on the milker-like prey-exploitation strategies. This may well be the evolutionary reason why many plant species channel so little of their energy resources into defense against herbivores (e.g., "cheap" carbon-demanding defenses rather than "expensive" nitrogen-demanding defenses), whether this be direct defense (Simms and Rausher 1987, 1989; Herms and Mattson 1992; Simms 1992) or indirect defense (Beattie 1985, p. 52; Dicke and Sabelis 1989). Hence, we hypothesize that boomerang coevolution constrains the plant's investment in direct and indirect defenses. Low investment, however, does not necessarily imply that plant defenses have a low impact. This entirely depends on the quantitative details of how the offensive and defensive traits of the interacting organisms at all three trophic levels settle evolutionarily. In other words, the impact of the plant's defenses increases if herbivores become more milker-like and predators more killer-like, and the impact decreases when herbivores become more killer-like and predators more milker-like.

22.5   Discussion

In this chapter we give a game theoretical view of the evolution of exploitation and defense strategies in tritrophic systems. Do we now understand why plants invest in promoting the effectiveness of the herbivore's enemies and can we learn from these insights to manipulate the virulence of the herbivore to the plant and that of the predator to the herbivore?

Are tritrophic systems prone to evolve conspiracy?

It is commonly believed that plant–predator mutualisms readily evolve because it is in the interests of both the plant and the predator to act against the herbivores (Price *et al.* 1980). Indeed, much evidence shows that plants can provide alternative food, shelter, and SOS signals utilized by the natural enemies of the herbivores, but what is still lacking is a critical assessment of the overall benefits to the plant. Much work is required to detect the role of cheating. Clearly, the plant cannot control who is benefiting from the facilities offered by the plant. Alternative food, shelter, and SOS signals are all open to "misuse" by the plant's enemies or inefficient natural enemies of the herbivores (Sabelis *et al.* 1999a, 1999b). In addition, there is a need to analyze how investments in plant defense influence competition among neighboring plants, since one plant may profit from the bodyguards retained and attracted by the other. Again, the investor cannot monopolize the benefits that accrue from bodyguards, since they move to wherever their victims are. Finally, the benefits to the plant depend on the number of predators in the surrounding environment and these numbers fluctuate. Costs and benefits of indirect plant defense are therefore expected to vary greatly in time and space (Bronstein 1994a, 1994b).

Thus, even though plenty of evidence shows that plants invest in attracting, retaining, feeding, and protecting bodyguards and that the bodyguards can make good use of the facilities offered by the plant, it is not an easy task to demonstrate in the field that predators assume the role of the plant's immune system.

Whereas a net benefit of indirect plant defenses is still to be shown experimentally, the rationale that underlies the evolution of indirect defenses is not fully established either. In this chapter we analyze the interaction between a plant, its neighbors, its herbivores, and the herbivore's enemies as a game of defense (among neighboring plants), escape (among herbivores), and resource exploitation (among herbivores and among predators). We explain that the mobilities of the herbivore and its predator play a crucial role in determining the extent to which a plant can reap the benefits from investing in direct or indirect defense (Tuomi *et al.* 1994). In addition, we discuss how prevailing resource exploitation strategies may change through metapopulation structure dynamics and migration via their impact on the probability of coinvasion of exploiters with different strategies of exploiting the resource. We argue that there is an interplay between plant defense, plant competition, exploitation of host plant, and prey in tritrophic systems. We also speculate that there is room for unstable evolutionary dynamics (e.g., boomerang coevolution), which may give way to selection for low investment in plant defense and milker-like predators. Indeed, empirical observations indicate that indirect defenses are not very costly, but killer-like, not milker-like predators seem to prevail in the field. This contrast between prediction and observation may indicate that predators have no control over the exploitation of their resources. This may arise from external causes, such as mortality through abiotic factors (wind, rain, fire) and competition with other natural enemies (pathogens, parasites, predators). To specify the conditions under which low-cost indirect defenses and killer-like predators evolve, our game-theoretical analysis needs extension to include evolution in the full tritrophic system and its interaction with ecological dynamics. This approach may lead to a more sound rationale for the "world is green" hypothesis. The commonly accepted hypothesis that mutualism readily evolves in plant–herbivore–predator systems because "it is both in the interest of plants to get rid of the herbivores and in the interest of the predators to find herbivores as prey" is as yet unfounded.

Perspectives for virulence management

Given that the theory on evolution and defense in tritrophic systems is rather immature, it is too early to consider direct applications, but there are several potentially important implications for virulence management. First, we may ask how two strategies, biological control and breeding for plant resistance, to combat plant pests influence ultimate success in crop protection. One-sided measures to increase direct plant defense may ultimately select for mild predators and, therefore, increased herbivory may be the end result. It seems wise to also breed for increased indirect defenses, because this promotes multiple colonization by predators, which will in turn select for increased predator virulence. Second, an old debate among

biocontrol workers is whether to release single or multiple species of predators. The latter seems best on the condition that it promotes local competition between predators, because this will increase their virulence. Third, we may wonder how mass rearing influences the virulence of predators before their release in the field. We suspect that mass rearings are like an undepletable prey patch and that leaving that patch is unlikely to promote within-rearing success. Hence, there will be selection for predators that suppress their tendency to disperse as long as there is food. This inadvertent selection for killer-like predators is good news for biological control workers aiming at fast suppression of the plant pest near the site of predator release, but are the aims of biological control over large areas served in this way, because at that spatial scale dispersal may become a vital trait of a successful biocontrol agent. Moreover, predators less efficient in clearing pest arthropods from a plant (milkers) may produce more dispersers and therefore promote their chances to reach distant sites. Clearly, there is every reason to reconsider carefully the criteria for a good biocontrol agent when the aim is to achieve control over a large spatial scale. Fourth, there is the long-standing question of where best to collect candidates for biological control. We expect to find milker-type predators near the borders of the geographical range (where predator densities are low) and killer-type predators in the center (where predator densities are high; see Pels and Sabelis 1999), but much more (theoretical and empirical) work is needed to substantiate this claim. A more elaborate discussion of these four implications is given in Chapter 32, albeit based on predictions of how selection molds predator virulence only and not on how it acts on virulence and defense in systems with three trophic levels.

Appendix 22.A   Evolutionarily Stable Herbivore Emigration Rate

Assume a metapopulation of patches with local interactions and global migration. As in Van Baalen and Sabelis (1995c), all the patches start with exactly the same number of predators and prey (metapopulation-wide equilibrium and no stochastic variation in the number of colonizers), that is, $N_0 = N(0)$ and $P_0 = P(0)$, and the redistribution of predators and prey occurs after completion of the local interaction (sequential interaction rounds). To assess the evolutionarily stable emigration rate (given r_N, k, and r_P), a measure of prey fitness is defined as the total number of herbivore emigrants per herbivore foundress, $w = m_N(N_{tot}/N_0)$, where N_{tot} is the total number of prey produced in a patch. Defined in this way, the fitness measure reaches an optimum between no migration ($m_N = 0$; extinction of all patches) and an emigration rate equal to the per capita growth rate ($m_N = r_N$; no offspring produced in the patch).

Further, assume that the two types of herbivore clones are attacked in proportion to their relative abundance, but that the mutant is so rare that $N_{res} + N_{mut} \approx N_{res}$. Then the herbivore dynamics in the patch are entirely dependent on the resident population and the rare mutant's presence does not influence the growth of the resident herbivore population. As a result of this last assumption the model yields an analytical solution for the fitness of the rare mutant. The dynamics of the rare mutant are given by

$$\frac{dN_{\text{mut}}}{dt} = \left(r_N - m_{N,\text{mut}}\right) N_{\text{mut}} - kP \frac{N_{\text{mut}}}{N_{\text{res}}} \ . \tag{22.7c}$$

Solving Equations (22.7a), (22.7b), and (22.7c) gives an explicit description of how the number of mutant herbivores changes with time,

$$N_{\text{mut}}(t) = \frac{N_{0,\text{mut}}}{N_0} \left\{ N_0 e^{(r_N - m_{N,\text{mut}})t} - P_0 \frac{k}{r_P - \left(r_N - m_{N,\text{res}}\right)} \right.$$
$$\left. \left[e^{(r_P + m_{N,\text{res}} - m_{N,\text{mut}})t} - e^{(r_N - m_{N,\text{mut}})t} \right] \right\} , \tag{22.7d}$$

with $N_{0,\text{mut}} = N_{\text{mut}}(0)$.

The fitness of the rare mutant w_m is the sum of dispersing mutants divided by $N_{0,\text{mut}}$,

$$w_m = m_{N,\text{mut}} \int \frac{N_{\text{mut}}(t)}{N_{0,\text{mut}}} \ , \tag{22.8a}$$

or

$$w_m = \frac{m_{N,\text{mut}}}{N_0} \left\{ N_0 \frac{e^{(r_N - m_{N,\text{mut}})\tau} - 1}{r_N - m_{N,\text{mut}}} - P_0 \frac{k}{r_P - \left(r_N - m_{N,\text{res}}\right)} \right.$$
$$\left. \left[\frac{e^{(r_P + m_{N,\text{res}} - m_{N,\text{mut}})\tau} - 1}{r_P + m_{N,\text{res}} - m_{N,\text{mut}}} - \frac{e^{(r_N - m_{N,\text{mut}})\tau} - 1}{r_N - m_{N,\text{mut}}} \right] \right\} . \tag{22.8b}$$

The evolutionarily stable emigration rate m_N^* can be found as the emigration rate of the resident population for which no mutant with a different emigration rate has higher fitness,

$$\left. \frac{dw_m}{dm_{N,\text{mut}}} \right|_{m_{N,\text{mut}} = m_{N,\text{res}}} = 0 \ , \tag{22.9}$$

Equations (22.8b) and (22.9) yield an implicit function, from which a solution for m_N^* can be obtained,

$$m_N^* = \frac{\left(N_0 + \frac{kP_0}{r_P - \Delta}\right) \left(\frac{e^{\Delta\tau} - 1}{\Delta}\right) - \left(\frac{kP_0}{r_P - \Delta}\right) \left(\frac{e^{r_P\tau} - 1}{r_P}\right)}{\left(\frac{kP_0}{r_P - \Delta}\right) \left(\frac{e^{r_P\tau} - 1}{r_P^2} - \frac{\tau e^{r_P\tau}}{r_P}\right) - \left(N_0 + \frac{kP_0}{r_P - \Delta}\right) \left(\frac{e^{\Delta\tau} - 1}{\Delta^2} - \frac{\tau e^{\Delta\tau}}{\Delta}\right)} \ , \tag{22.10a}$$

where $\Delta = r_N - m_N^*$ and τ is the total time of the predator–prey interaction,

$$\tau = \frac{1}{r_P - \Delta} \ln \left(1 + \frac{r_P - \Delta}{k} \frac{N_0}{P_0}\right) \ . \tag{22.10b}$$

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