Minus van Baalen. *Evolutionary Stability and the Persistence of Predator-Prey Systems.*
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Introduction

Predator-Prey Systems

Even though herbivorous spider mites are so small that they are difficult to see with the naked eye, the damage they cause is dreaded by those who keep plants in the window-sill and, of course, by growers. While becoming covered with a sticky web, plants get a wilted, yellowish appearance and if nothing is done about it, the plants soon die. In the home spider mites are a nuisance, but in agriculture they may constitute a serious economic problem.

One of the ways to combat spider mites is to release predatory mites. Under the favourable conditions of a large prey population, predatory mites multiply fast and within days or weeks there is a large population of predators, rapidly decimating the spider mites. In a glasshouse, biological control using predatory mites is often so effective that it results in the complete extermination of the prey. To the grower this is a bonus, but to an ecologist it poses an important question. Why do prey and predators go extinct? Why do the predators overexploit their own means of subsistence?

Questions like these are not only of academic interest. Repeated release of predatory mites may be feasible in a glasshouse, in other cases biological control hinges upon the ability of predators to keep their prey at a low level while not exterminating it. This is not an impossible aim. Many organisms that cause damage in agriculture are kept in check by natural enemies in their original habitat. Apparently prey and predators do persist in their natural habitat, but *how* is still an unresolved issue.

Ecologists have formulated and analysed many models for the interaction of predator and prey, to assess how persistence is affected by various ‘factors’, like spatial structure of the environment, the presence of alternative food sources for the predators, the presence of refuges for the prey, and so on. From such exercises it has become clear that persistence is by no means an inevitable outcome—there is no such law as ‘the ecological equilibrium of prey and predator is always stable’—because oscillations of predator and prey may become so violent that eventually one or both of the populations dies out. Furthermore it has become clear that the population dynamical outcome may strongly depend on the properties of prey and predators. For example, in biological control it can make a large difference whether predators specialize on the pest species, or whether they also consume other food sources.

In this thesis, one will find no practical directives for how to carry out biological control programs. Indeed, one will not find many references to mites, even though mite predator-prey systems originally provided the impetus for the research. Instead, the chapters deal interacting populations in a variety of settings. What unifies the chapters is the approach rather than the subject: the attempt to integrate population dynamical analysis and evolutionary theory.

A population dynamical model is the combination of a set of rules describing the behaviour of individuals and a bookkeeping mechanism to keep track of population sizes over time. Usually, the set of rules describing individual behaviour is based on assumptions, and this confers a certain arbitrariness to the model; even when observations or experiments underlie the assumptions, uncertainty often makes it necessary to allow quite a margin. When population dynamical analysis is combined with evolutionary theory, one can replace assumptions by an evolutionary argument. This way, one can form hypotheses about population dynamics that will result if populations are subject to natural selection.

Population Dynamics

Population ecologists do not formulate models in search for a ‘grand unified theory’; this would be a senseless undertaking given the enormous diversity among ecological systems. Instead, the models they formulate serve to provide arguments, next to experiment and observation, in an on-going debate about which factors are most important in determining the large-scale behaviour of predator-prey systems or more complex ones. In the course of this debate, many hypotheses have been formulated, and many of these have been put to test, first by observing behaviour to estimate model parameters, and then by testing predicted population dynamics. This, however, is a complex business. A population dynamical model is usually highly simplified compared to the world outside. Comparing a population dynamical analysis with data obtained from experiment or observation is therefore often problematic. It is very difficult to provide unambiguous data in favour of a hypothesis, and it is relatively easy to provide alternative hypotheses for these data.

The conclusions derived from a population dynamical model are no more ‘hard’ than are the assumptions that underlie it. Using evolutionary arguments to explain individual traits instead of merely assuming them may help to sharpen ecological hypotheses.

Evolutionary Ecology

Given the success of Darwin’s theory of evolution caused by natural selection, it may be a surprise that, especially in ecology, evolutionary arguments have long been little employed, and if they were, usually only verbally. Ecologists may have hesitated to include evolutionary arguments on the ground that ecology is so complex that we should first understand how an ecosystem works before we will be able to understand how it evolves. Nonetheless, during the last 20 years or so, the branch called ‘evolutionary ecology’ has gained more and more impetus. At first the focus was at explaining the evolution of traits instead of merely assuming or observing them. Recently, more effort is being devoted to understand the population dynamical consequences of behaviour that has evolved under natural selection.

Basically, the problem is to determine what to expect if populations are subject to natural selection. As is widely assumed, evolution proceeds because new mutants may arise, slightly different from their ancestors. Most mutants will do worse than their parents, but if a mutant is successful it will invade the population, and may eventually replace its ancestral population. This process will go on until a situation is reached in which no new mutant can do better than the type that is predominant in the population. This situation is called 'evolutionary stability'. It will be clear that the analysis of evolutionary stability is a great tool to formulate hypotheses about behaviour that has evolved under natural selection.

The first step in the analysis is to consider all possible options, or 'strategies', and then work out which strategy an individual should adopt to maximize its fitness, *i.e.*, maximize its contribution to the next generation. In many cases, the optimal strategy does not depend on the strategies adopted by other members of the population. In other cases, in particular in interacting populations, the optimal strategy does depend on what strategies prevail. Consider, for example, the defence of prey against predators. If the prey population at large invests heavily in anti-predators traits, the predator population fares less well, and may reduce in density. But then the risk of predation will decrease, which creates opportunities for mutant prey that invest less in defence and produce more offspring instead. When such mutants do better than their heavily-defended conspecifics, average level of defence decreases—to the benefit of the predators. Therefore, to explain the level of defence among the prey, one should take into account how predators mediate interactions among the prey.

The chapters of this theses provide more worked-out examples of the interdependence of population dynamics and evolution. In this introduction I will discuss the first chapter in somewhat more detail, as it outlines the basic approach. Then I will discuss the remaining chapters more briefly.

Uneven Spatial Distributions

In the 1930s Nicholson and Bailey formulated a simple population dynamical model for predator-prey interactions with non-overlapping generations. Their model turned out to be extremely unstable; an ecological equilibrium of prey and predator exists, but even the slightest perturbation is enough to start a series of increasing oscillations that leads, within a few generations, to the extinction of both prey and predators (Fig. 1). This finding spurred much research, because predator-prey interactions with non-overlapping generations are very common, and somehow these persist. What essential aspect or aspects were overlooked in Nicholson and Bailey's simple model? Inspired by observation, various modifications of the model were proposed, some of which appeared to promote persistence. But none of these modifications captured the imagination so much as Hassell and May's variant proposed in the 1970s: *if* the prey population is spread unevenly over space, and *if* the predators concentrate searching in the areas harbouring most prey, *then* oscillations would be damped and the ecological equilibrium of prey and predators would be stable (Fig. 2). This model seemed to be very generally applicable. Most prey populations *are* unevenly distributed; uneven spatial distributions even are the rule rather than the exception. Moreover, predators *do* preferentially forage in the most profitable patches. Thus, the 'aggregative response' of predators to prey density could very well be a very general persistence-promoting mechanism.

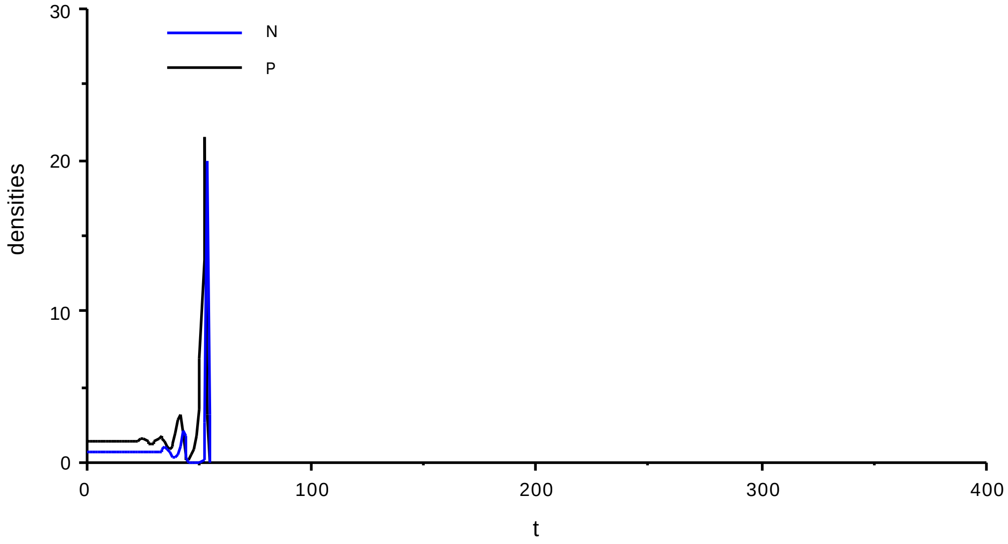

Figure 1 Nicholson and Bailey's model predicts unstable dynamics leading to extinction of prey (*N*) and predators (*P*).

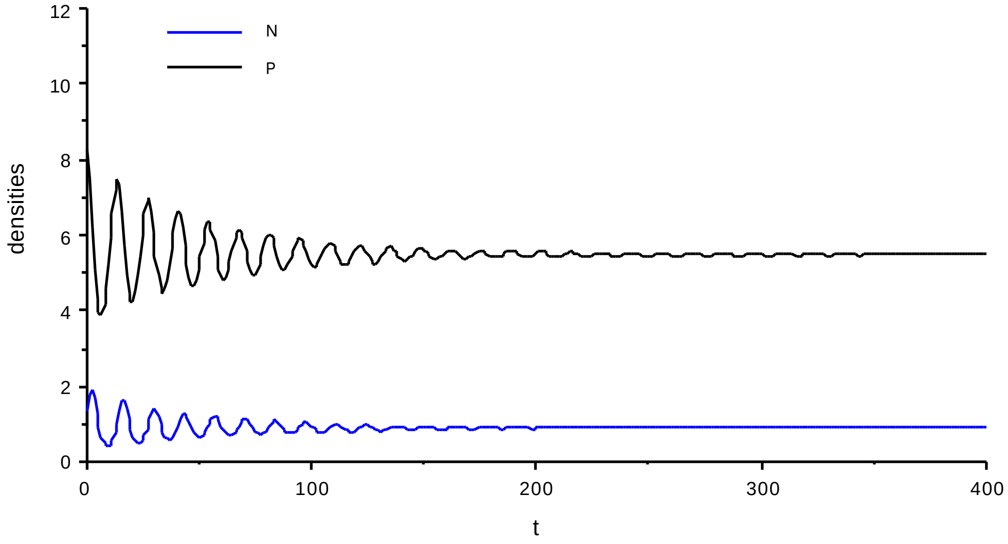

Figure 2 According to Hassell and May's variant of Nicholson and Bailey's model, uneven spatial distributions may lead to a stable population dynamical equilibrium of prey (*N*) and predators (*P*).

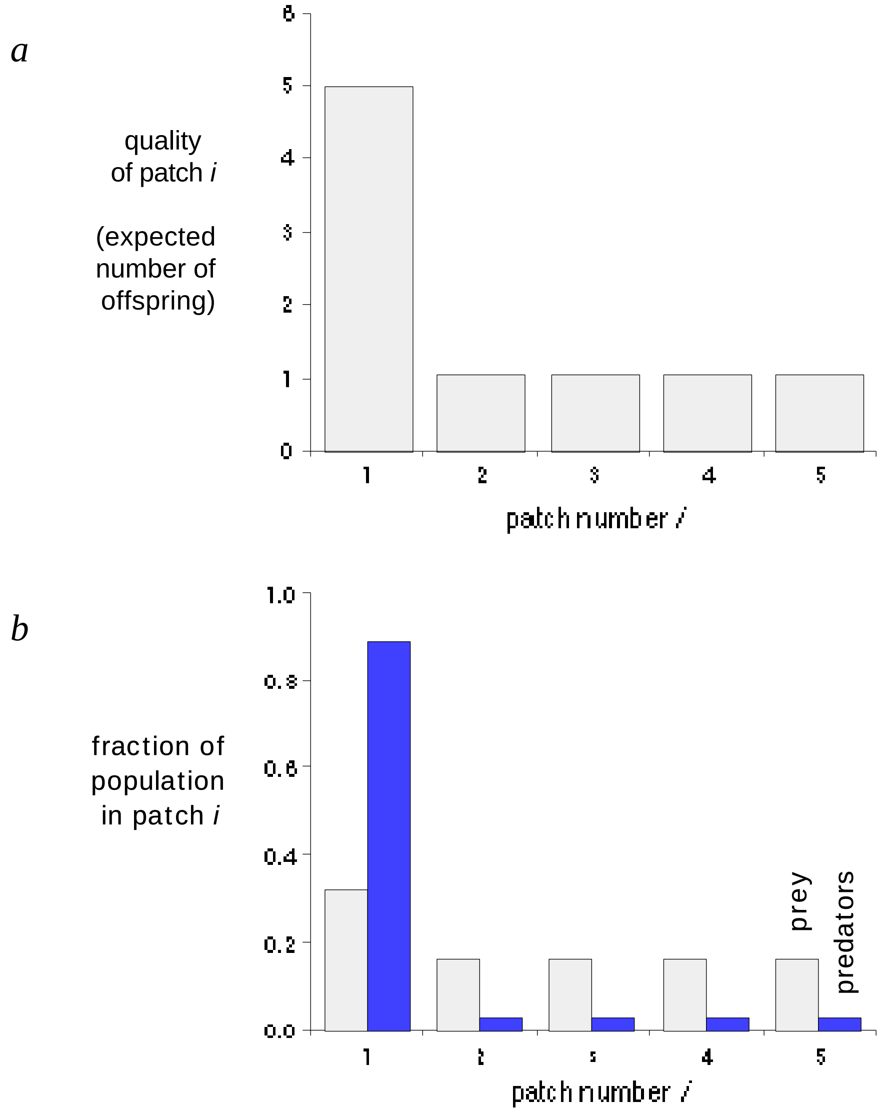

Figure 3 Differences in patch quality (*a*) leading to uneven spatial distributions (*b*) when prey and predators adopt evolutionarily stable patch selection strategies. Such uneven spatial distributions are necessary to lead to a stable population dynamical equilibrium (as shown in Fig. 2). If differences in patch quality are less, it pays prey to avoid the high-prey-density patch—resulting in a more even distribution of the prey. Then natural selection will favour predators that aggregate less strongly—and unstable dynamics of the type of Fig. 1 result.

Many population ecologists set off to test this hypothesis, by observing spatial distributions of prey, by studying the foraging behaviour of predators, and so forth. A confusing picture emerged, and a debate was started that continues to this day. Of course, uneven prey distributions were found, and predators appeared to have elaborate tactics to search for their prey. What remained a question, however, was whether the strength of the aggregative response would be sufficient to promote persistence. As Hassell & May's model was not designed to describe a specific natural system, but rather to demonstrate the potential consequences of a single factor (spatial distribution) this is not an easy question to decide.

What one can do (as elaborated in Chapter 1 of this thesis) is try to extend Hassell and May's analysis with an evolutionary argument. Hassell and May's model may be a simple 'toy world' inhabited by simple organisms, natural selection will operate there all the same. Do spatial population distributions as were assumed by Hassell and May result from searching strategies (of either predator or prey) that are favoured by natural selection?

Consider first evolution of predators only, and take the uneven distribution of the prey as given. Obviously, a single predator should forage in the patch containing most prey. However, if a large number of other predators will do the same, natural selection may actually favour predators that escape the crowd and forage in low-prey-density patches! Thus, natural selection will put an upper bound to the strength of the 'aggregative response', and this means that the scope for persistence is reduced.

When not only the predators evolve but also the prey, the situation changes profoundly. Prey will do best by avoiding patches with a high numbers of conspecifics, because most predators will be found there. An illustration is given in Figure 3 (which is the same as Fig. 5 from Chapter 1). It depicts a hypothetical environment consisting of five patches of food for the prey, where one of the patches is of much better quality (Fig. 3*a*). In absence of predators, the prey will obviously do best by moving to patch number one. But if all prey

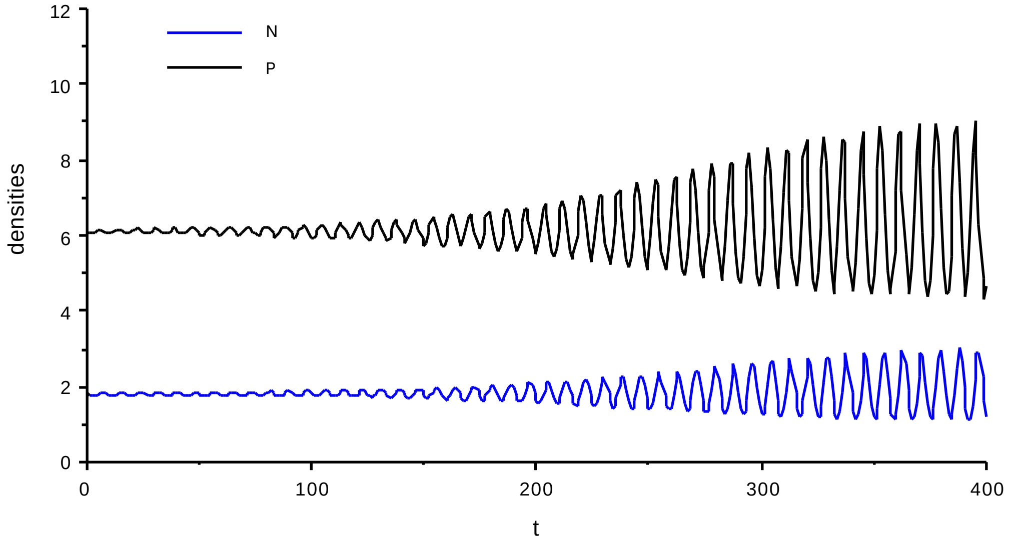

Figure 4 If predators can react to variations in prey and predator density, whereas prey can detect patch quality only, the stable equilibrium may give way to a limit cycle, *i.e.* regular oscillations of prey (N) and predators (P).

move into a single patch, the predators will all follow. Then the better quality of the patch may completely offset by the risk of predation, which means that a mutant prey that selects one of the low-quality patches will get more offspring. The prey strategy to select patch one is therefore not evolutionarily stable. But then, if enough prey seek refuge in the low-quality patches, a mutant predator that selects one of the a low-quality patches can invade. Eventually evolution will lead to a situation in which it pays for no individual to prefer any one patch over another. This situation is depicted in Figure 3*b*. It can be seen that for uneven spatial distributions (light shading: distribution of the prey; dark shading: of the predators) a large difference in patch quality must be assumed. As ecological stability requires population distributions roughly of the type as shown in Figure 3*b*, the conditions for ecological *stability* are quite narrow.

Non-equilibrium persistence

If the population dynamical equilibrium of predator and prey is stable, predator and prey are likely to persist—obviously. However, this does not mean that an unstable population dynamical equilibrium will always lead to extinction. Indeed, population dynamical analysis has revealed that in many cases populations remain fluctuating but nevertheless do not go extinct even in the long run. Such fluctuations may be regular (which is called a limit cycle, see Fig. 4) or irregular (in which case the dynamics are called chaotic, see Fig. 5).

In Chapter 1 we concluded that the conditions for a stable ecological equilibrium of prey

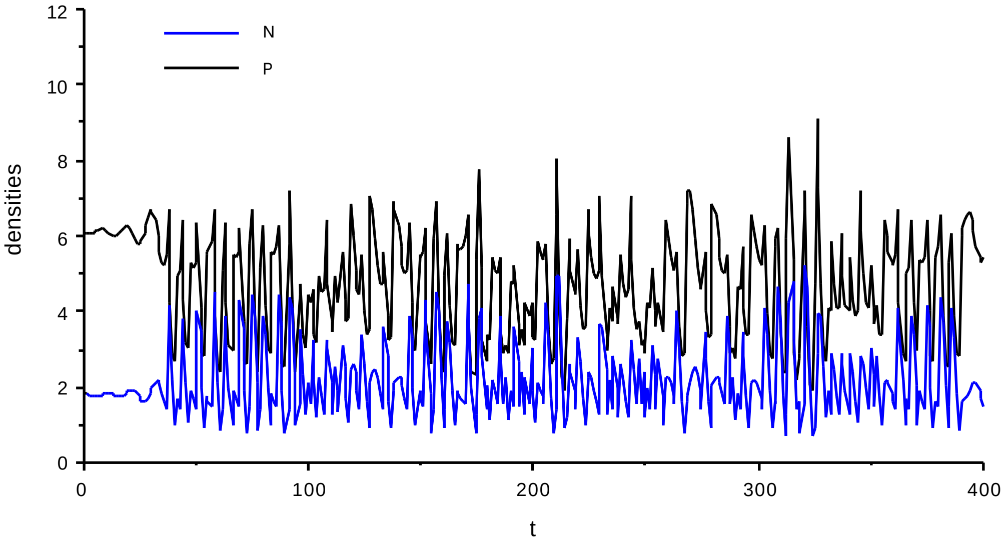

Figure 5 If prey and predators react to each other’s spatial distribution, the population dynamical result may be chaos, *i.e.* *ir*regular oscillations of prey (*N*) and predators (*P*).

and predator were quite narrow. But we found that the conditions for non-equilibrium persistence—in the form cyclic or chaotic fluctuations—may occur in a much wider range of conditions (Chapter 2). This holds especially when predators and prey can *flexibly* react to their surroundings—that is, seek out the best patches depending on the circumstances. This conclusion would suggest that the refined abilities of many prey and predators to assess and react to their environment may have far-reaching consequences; the availability of information will then be an important factor determining population dynamics.

Alternative Food

Almost all consumers (predators, herbivores) live among a variety of potential food sources, yet most of them consume on only a few food sources or even specialize on a single one. Why is that so? Optimal foraging theory tries to determine what foraging strategies will be favoured by natural selection. Which types should a consumer include in its diet and which should it ignore, to maximize its fitness? Being based on an evolutionary argument, optimal foraging theory is an old but thriving branch of evolutionary ecology.

Most models of optimal foraging theory assume that the abundance of the various food types is constant. In many cases this is a reasonable assumption, but in many other cases, diet choice will affect the food types' abundances. Then an answer requires the combination of optimal foraging theory and population dynamics. In Chapter 3, a simple situation is analysed, in which only one food source is affected by predation (the prey) while another food source (alternative food) is present in constant amounts. Many arthropod predators, including predatory mites, can switch to various—ubiquitous—alternative food sources if their preferred prey is scarce.

From analyses of population dynamical models it was already known that some types of switching behaviour may lead to a stable population dynamical equilibrium of predator and prey. However, other types of switching behaviour lead to an unstable equilibrium. In Chapter 3 we pose ourselves two questions: (1) what will be the effect of switching behaviour that is predicted by optimal foraging theory? and (2) what happens if the equilibrium is unstable?

Optimal foraging predicts a sharp switch: if there is sufficient prey, predators should ignore alternative food completely; if there is not sufficient prey, predators should consume everything they encounter. Such sharp switches do not promote stability, stability only results if predators change their diet in a continuous fashion. Nevertheless, persistence appears to be promoted under a much wider range of conditions. As long as predators ignore alternative food, oscillations of prey and predator will increase in amplitude. At some point, however, prey becomes so scarce that predators include alternative food into their diet. Then, the predators will starve less rapidly and the prey is relieved from predation pressure, a combination of effects which prevents the oscillation from further divergence and a limit cycle results. Thus, the importance of alternative food may lie not so much in the fact that it may promote stability, but rather that it prevents unbounded oscillations.

Metapopulation Dynamics

The first three chapters of this thesis deal with evolution in ‘single’ predator-prey systems: a single population of prey interacting with a single population of predators. One of the conclusions is that a stable population dynamical equilibrium of prey and predators may be among the outcomes, but not *a priorily*. In other cases evolution will lead to populations that persist in a fluctuating way, whereas again in other cases predator or prey will go extinct.

If a single predator-prey system is unstable, interesting things happen when predator and prey are spread over a large region in space. Then, provided individuals move through space relatively slowly, different regions may start to oscillate out of phase. This means that in some regions prey density will be high, while in other regions prey will be virtually absent. A map of the prey population will then show local ‘patches’ of high prey density surrounded by regions devoid of prey; a similar map can be made of the predator

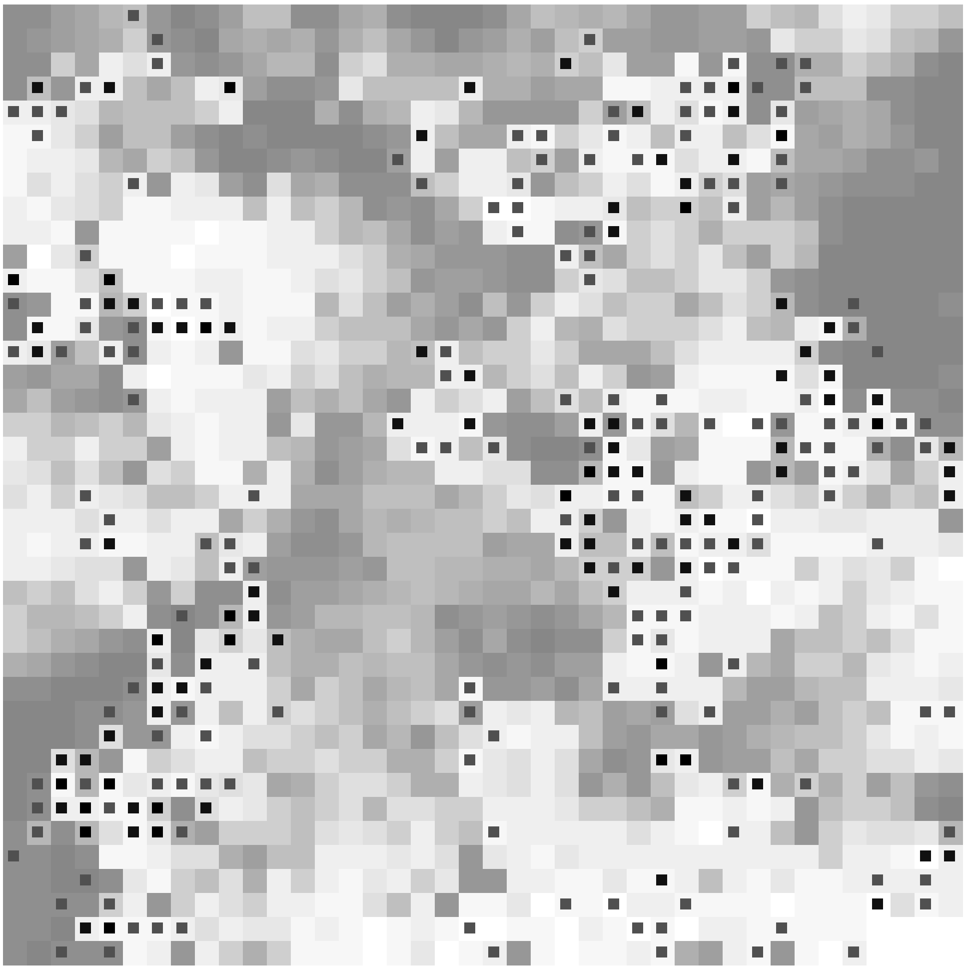

Figure 6 A map of a spatially distributed predator-prey system: shading intensity indicates local prey density, black dots show the distribution of the predators.

population (see Fig. 5 for an example). Such maps will not remain static, of course. Patches of prey will grow and expand. Eventually they will be found and invaded by predators. These predators rapidly multiply, and finally reduce local prey density again. Having depleted the local prey patch, the predators must then search for other patches of prey, that may have been founded in the meantime. This process closely resembles what happens in many mite predator-prey systems.

If predators completely wipe out the prey locally, prey and predator can persist only in a larger whole. Such a dynamic ensemble of local populations that get extinct and become recolonized is called a metapopulation. Metapopulations are of considerable interest, not only for mite predator-prey systems, and have been studied extensively. Should conservation biologists strive for many small nature reserves or just a single big one, when they want to preserve a rare species? The chances that it gets extinct are probably smallest in a big patch, but if it gets extinct it is lost. In an ensemble of patches local extinction will occur more frequently, but empty patches may be recolonized from neighbouring patches.

In a predator-prey metapopulation, natural selection may favour other traits than in a single, ‘well-mixed’ system. In a well-mixed system, natural selection will favour predators that maximize their prey capture rate—because this will result in most offspring. In a metapopulation this may be different. Consider a lucky predator that has just found a new, expanding prey patch. It will start a local population that is exploiting the prey patch. If the predator and its descendants maximize prey capture rate, they should all stay within the prey patch, until they have consumed all prey and have to leave in search of new prey patches. However, there are other strategies strategies to exploit a prey patch. Consider a predator whose descendants have an innate tendency to leave the patch before the prey are extinct. From the viewpoint of the individual, dispersing is a stupid thing to do—after all, why abandon your food if it is uncertain that you will find food elsewhere?—but dispersal helps relatives that stay behind; the local prey population is exploited less heavily and will exist for a longer time. By the time ‘milkers’ have finished the local prey population, the milker foundress will have many more descendants roaming the area than has the ‘killer’ foundress whose descendants all stayed within the patch as long as possible.

The potential advantages of milking are thus very great. But there are disadvantages too: if a milker patch is invaded by a killer, the killer and its descendants quickly consume all prey, spoiling things for the milkers in the patch. It therefore only pays to adopt the milker strategy instead of the killer strategy only if the risk of invasion is rather low. But then, if more predators become killers the risk of invasion decreases—after all, killers do not exploit prey patches in an efficient way and consequently their overall abundance will be low—and the conditions for milkers improve again. Thus there is a balance determining optimal strategies for the exploitation of a prey patch. (This balance is investigated in more detail in Chapter 4.)

If one replaces the terms ‘prey patch’ and ‘predator’ by ‘host’ and ‘parasite’, an interesting analogy arises. A parasite (bacterium, virus or other pathogen) can be said to exploit a host in much the same way as a predator ca be said to exploit a prey patch. When an infective stage enters a host, it multiplies within the host, giving rise to a population of descendants—that is, to a clone. This clone then produces new infective stages to achieve transmission to new hosts. Just as there are different ways to exploit a local prey population, parasites can exploit a host in different ways. ‘Virulent’ parasites are literally ‘killers’—they opt for quick reproduction to the detriment of their host. ‘Avirulent’ parasites are more of the ‘milker’ type—they reduce ill effects in order to keep their host longer alive. If a parasite clone can monopolize its host, it pays to exploit its host most efficiently—that is, it pays to be avirulent. If a clone has to share its host with other clones, increased virulence is favoured—an attempt to prolong the host’s infective period is ineffective if the other clones do not cooperate. Now if there is a clear case where population dynamics and natural selection are interdependent, it is the case of parasite virulence. When the parasites in the population are avirulent, their efficient host use leads to a high prevalence in the host population. Under population dynamical equilibrium, the ‘force of infection’ is high, which means that the fraction of hosts harbouring multiple parasite clones is also likely to be high; more virulent parasites do better than avirulent ones. However, a change in virulence has population dynamical consequences; more virulent parasites have a lower equilibrium prevalence (less efficient host-use!). This change in population dynamics has, in turn, evolutionary consequences; low parasite prevalence means that the force of infection will be low, which improves conditions for avirulent parasites—they run less risk to lose their host. Thus, the evolution of virulence will be mediated by changes in population dynamics.

Usually, population dynamical models for the interaction between hosts and parasites do not take multiple infection into account. This is a sensible simplification because the arrival of a new parasite individual in a host harbouring a whole population already is unlikely to have many effects. However, for an understanding of the evolution of virulence, multiple infection (or, more precisely, within-host competition among the parasites) should not be ignored. If hosts are infected by single parasite clones, natural selection will favour avirulent ones, whereas if hosts are infected by multiple clones, increased virulence is favoured.

Epilogue

Analysis of population dynamical models may lead to insight in how the traits of individuals affect the dynamics of the system they are part of. This, however, does not reveal the likelihood that such traits actually occur. As different traits will often result in different population dynamics, any arbitrariness in the traits immediately translates into arbitrariness of the predictions of the model. In the first place, combining analysis of population dynamics with evolutionary arguments may help to sharpen existing ecological hypotheses. For example, Hassell & May’s prediction that uneven spatial distributions of predator and prey promotes population dynamical stability will hold only under a rather narrow set of conditions if predator and prey evolve under natural selection. Thus, the so-called ‘aggregative response’ of predators (most predators will be found in the most profitable prey patches) may be not so general a stabilizing mechanism as it initially seemed. As another example, combination of population dynamics with optimal foraging theory, suggests that the presence of alternative food (next to prey) may promote non-equilibrium persistence rather than stability of the equilibrium.

In the second place, combination of population dynamical and evolutionary analysis may lead to new hypotheses. Many predator-prey metapopulation models assume that local populations are founded by a single colonist. However, when then also evolution in a metapopulation is considered, it appears that different traits may be favoured by natural selection than are assumed by the modeller. For example, *if* all local predator populations are started by a single individual one would expect that they will prudently exploit their local prey population. Many predatory mites do not appear to be such ‘prudent predators’—thus one would predict that local populations have more than one foundress, Thus, for a more full understanding of predator-prey metapopulations, one should try to get more insight in the frequency of multiple invasion and the strength of within-patch competetion.

This thesis provides a number of illustrative cases of how evolution and population dynamics interact. Many interesting problems wait to be tackled. For example, under what conditions do interacting monomorphic populations break up into polymorphic populations? One will need to investigate how the conditions for divergence interact with population dynamics. Recent developments in theoretical biology may provide new mathematical tools. How will spatial pattern in a spatially structured population change when individuals evolve, and how is, in turn, evolution affected by such pattern? Computer simulations that keep track of family lineages in spatially structured predator-prey interactions may lead to new insight into this question. And, eventually, all this effort may help us understand better why spider mites and predators persist in one case, and go extinct in the other.