Foraging under incomplete information:

parasitoid behaviour and community dynamics

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Stellingen

1. De geurstoffen die een plant verspreidt in reactie op vraatschade kunnen bij sluipwespen zowel voordelige als nadelige gedragsresponsen veroorzaken. Men kan deze plantengeuren dan ook niet uitsluitend als synomonen beschouwen.
   Dit proefschrift

2. Het in zijn geheel besproeien van een gewas met jasmonzuur kan het uitsterven van specialistische natuurlijke vijanden in dat gewas veroorzaken.
   N.a.v. Thaler, J.S. (1999) Jasmonate-inducible defences cause increased parasitism of herbivores. Nature 399: 686-688, en dit proefschrift

3. Er is onvoldoende onderzoek gedaan om te kunnen bepalen of de trofische cascade die bij effectieve biologische bestrijding in een monocultuur optreedt, ook voorkomt bij een complexe mengteelt van gewassen.

4. In voedselweb-studies worden interactie-sterktes nog vaak gereduceerd tot een gemiddelde. Het verdient aanbeveling de dynamiek van interactie-sterktes te bestuderen, zowel in een voedselweb als in het informatieweb dat daarmee samenhangt.

5. Het boek *Consciousness explained* (1991) van Daniel C. Dennett verklaart het bewustzijn niet.

6. Een 'Index of Cooperative Effort' (ICE) zou naast de aantallen publicaties en citaties een belangrijke rol moeten spelen bij het beoordelen van individuele wetenschappers.

7. Als sluipwespen ook populaties van mensen zouden reguleren was de wereld nog veel groener.

8. Beton maakt meer kapot dan je lief is.

9. Om de evenhoevigen op de Veluwe te beschermen tegen MKZ moet de productie van vlees in Nederland ophouden of kleinschaliger worden.

Stellingen behorende bij het proefschrift van Matthijs Vos
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Abstract

This thesis describes research on multitrophic interactions between parasitoids, herbivores and plants. These are all involved in a dynamic game of hide-and-seek. Insect herbivores may occur in different spatial distributions across plants. Some species occur in local clusters, while others have a more even distribution. Parasitoids are challenged to deal effectively with such variation in the spatial distribution of their victims. I studied how different species and strains of *Cotesia* parasitoids make use of chemical information and foraging experience under varying spatial distributions of hosts.

The parasitoids *Cotesia glomerata* and *Cotesia rubecula* show clear interspecific variation in foraging decisions when exploiting patches with herbivores. *C. glomerata* tunes its foraging decisions to the current environment as it gains experience with hosts during subsequent patch visits. In contrast, foraging decisions in *C. rubecula* seem insensitive to acquired experience. These *Cotesia* species prefer different herbivore species, that occur in different spatial distributions across plants. *C. glomerata* prefers to attack *Pieris brassicae*, that occurs in rare clusters of highly variable density. The parasitoid *C. rubecula* specialises on *Pieris rapae* that mostly feeds solitarily on plants. This leads the parasitoid *C. glomerata* to experience a more variable environment, with a wider scope for increased efficiency through learning.

Both *Pieris* species are present in Europe, but the clustered host is absent in North America. The parasitoid *C. glomerata* was introduced to North America in 1883 to control solitarily feeding *Pieris rapae*, and about 350 generations of *C. glomerata* parasitoids have now foraged there. The experimental results suggest that American *C. glomerata* have adapted to forage for solitary host larvae, mostly through a loss of costly traits for finding rare clustered larvae. The European parasitoids spend a lot of time on explorative flights, while their American conspecifics seem to minimise travel costs and effectively focus on the exploitation of patches with solitary hosts.

Herbivores are hard to find victims for parasitoids, and parasitic wasps may use any reliable information from the environment to locate them. Plants play a key role in providing this information. Plants may emit volatile infochemicals, when they are damaged by herbivores. Such volatiles are attractive to parasitoids and may guide them to their hosts. However, this research shows that the reliability of plant infochemicals may be very low when a complex of herbivores feeds on the plant. This is important, as plants are mostly attacked by several herbivore species, both in agricultural and natural ecosystems. The presence of nonhost herbivores causes parasitoids to waste time on damaged plants without hosts. A model study shows that the interaction between this 'wasted time' effect and herbivore diversity stabilises communities of parasitoids and herbivores. However, above a certain diversity threshold parasitoids may waste too much time on nonhost herbivores. This may lead to the local extinction of several parasitoid species. Thus, diversity may promote both stability and extinctions, when plants provide unreliable information.

This thesis shows that the flow of information between all these actors is crucial for the understanding of insect behaviour and community dynamics. This information flow involves plants, parasitoids and, surprisingly, both host and nonhost herbivores.

Voor mijn ouders

Voor Lea

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1

Hide-and-seek on entangled banks

It is interesting to contemplate an entangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent on each other in so complex a manner, have all been produced by laws acting around us. These laws, taken in the largest sense, being growth with reproduction; inheritance which is almost implied by reproduction; variability from the indirect and direct action of the external conditions of life, and from use and disuse; a ratio of increase so high as to lead to a struggle for life, and as a consequence to natural selection, entailing divergence of character and the extinction of less-improved forms

...and that whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being evolved.

-Charles Darwin
1859 On the origin of species by means of natural selection

GENERAL INTRODUCTION

Parasitoids are important in terms of species richness, ecological impact and economic importance (LaSalle & Gauld 1991, 1993; Pickering & Sharkey 1995) and as model organisms in evolutionary and ecological studies (e.g. Godfray 1994; Jones *et al.* 1995; Abrahamson & Weis 1997; Hassell 2000). Female parasitoids forage for insects to use these as hosts, a food source for their offspring. The larvae of many parasitoid species eat their host from the inside, in order to complete development. Successful parasitoid development causes hosts to die and adult parasitoids to emerge. Estimates on the exact number of species on earth are of limited accuracy (May 1998), but parasitoids have been estimated to comprise at least ten percent of all known animal species (Rothschild 1965; Askew 1971; Hassell 1978) or between 170.000 and 6 million species (LaSalle & Gauld 1991). Food webs comprising green plants, insect herbivores and insect parasitoids include over half of all known animal[1] species. Gaining insights in their functioning and structure could provide a basis for deeper understanding of terrestrial communities (Price 1980; Strong *et al.* 1984; Hawkins & Lawton 1987). Parasitoids may regulate herbivorous insects in natural ecosystems and thus assist in keeping the world a green place. Some studies fail to find such regulation (see e.g. Dempster 1983), but this may partly be due to methodological difficulties in the detection of density dependence of parasitism (see Hassell 1986). However, an analysis of classical biological control projects in agro-ecosystems indicates that parasitoids often do control herbivore populations, with more than 216 projects in 99 countries achieving complete or satisfactory pest suppression (Greathead 1986). In this light some authors consider parasitoids to be keystone species in many terrestrial ecosystems (LaSalle & Gauld 1991, 1993).

Multitrophic interactions

Plants, herbivores and parasitoids are involved in a multitrophic game of hide-and-seek, in which infochemicals and the spatial distribution of host and nonhost herbivores play a key role. Female parasitoids are under selection to efficiently spend their limited time on the location and exploitation of hosts, which often occur in patches (Godfray 1994; Ellers *et al.* 2000). The adequacy of foraging decisions in female parasitoids is directly linked with reproductive success. This makes these animals highly suitable for evolutionary studies of foraging behaviour (Cook & Hubbard 1977; van Alphen & Vet 1986). Hosts for their part are under strong selection not to be found by their parasitoids (Vet *et al.* 1991; Vet & Dicke 1992). Hosts release only small amounts of volatiles (Turlings *et al.* 1991a), which reduces their detectability for parasitoids at longer distances (Vet *et al.* 1991).

An important characteristic determining the chances of being located and attacked, is the 0spatial distribution of hosts. Herbivorous hosts may be relatively inconspicuous when they occur solitarily on plants (Mauricio & Bowers 1990). On the other hand, hosts may experience a

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[1] metazoans (multi-cellular animals)

reduced per capita risk of parasitism when occurring in large aggregates (Hunter 2001). This might be due to group defence behaviour (Stamp 1981; Vulinec 1990), or to dilution effects and the limited accessibility of central individuals within a cluster (Turchin & Kareiva 1989). Gregarious and solitary feeding by herbivorous insects will lead to different patterns of damage on plants, thus providing visual information to parasitoids in search of hosts (Wäckers 1994).

In addition, feeding by herbivores induces the production and emission of a bouquet of volatiles in many plant species (Vet & Dicke 1992). Such synomones are attractive to natural enemies and are considered to guide parasitoids and predators to their herbivorous victims (Vet *et al.* 1991; Vet & Dicke 1992). A potential drawback of herbivore-induced volatile emission may be that it makes plants more conspicuous to other herbivores (Dicke & Vet 1999). Plants are able to emit volatiles in relatively large quantities, which makes a plant-herbivore-complex more detectable to parasitoids than hosts and their by-products (Turlings *et al.* 1991b; Vet *et al.* 1991; Steinberg *et al.* 1993; Geervliet *et al.* 1994). Plants may respond differentially to different species and densities of herbivores in their intensity of volatile production (see Geervliet *et al.* 1997). Such differential responses may affect how conspicuous clustered or solitary herbivores are to foraging parasitoids.

Some plants emit specific volatile blends for different herbivore species, and thus selectively attract parasitoids (Du *et al.* 1996; De Moraes *et al.* 1998). However, several parasitoid species are attracted to plants and leaves infested with non-host herbivores (Agelopoulos & Keller 1994; Geervliet *et al.* 1996). The volatile blends from these plants may be non-specific or very similar for different herbivore species (Geervliet *et al.* 1997; Dicke & Vet 1999). The majority of plant species in the field will be attacked by a complex of herbivores (Lawton & Schröder 1978; Futuyma & Gould 1979; Futuyma 1983). Interspecific associations of herbivores on plants may reduce the reliability of plant volatile information and exploit this to reduce the chances of location by specialist natural enemies. These have to face such complications and deal with the presence of herbivores that are outside their diet.

The literature abounds with experimental studies on infochemical use by parasitoids (e.g. Waage 1979; Noldus *et al.* 1991; Steinberg *et al.* 1992; Vet & Dicke 1992; McCall *et al.* 1993; Wiskerke *et al.* 1993; Agelopoulos & Keller 1994; Geervliet *et al.* 1994; Agelopoulos *et al.* 1995; Potting *et al.* 1995; Geervliet *et al.* 1996; Colazza *et al.* 1997; Geervliet *et al.* 1998a,b; Jang *et al.* 2000).

Experimental research on behavioural variation in response to variation in host distributions is much scarcer, but see Wiskerke & Vet (1994); Driessen *et al.* (1995); Driessen & Bernstein (1999). In this thesis we investigate both interspecific and intraspecific variation in parasitoid foraging behaviour. We study the mechanisms underlying parasitoid foraging decisions and evaluate whether we can infer adaptive variation in the way parasitoids deal with the spatial distribution of their hosts. The system consists of European and North American *Cotesia* parasitoids of *Pieris* caterpillars that feed gregariously or solitarily on cruciferous plants.

Before presenting my data I will first provide a theoretical background of the behavioural and evolutionary ecological approach. Next I will address theoretical aspects of foraging for hosts with different spatial distributions, and the value of information to a parasitoid during foraging. A third section provides information on the spatial ecology of the experimental system. Finally I state the general objectives of this thesis and introduce the research described in each of the following chapters.

THEORETICAL BACKGROUND

Adaptation

Life on earth was already extant about $3{,}5 \cdot 10^9$ years ago (Schopf 1993). Since then many new types of organisms have replaced other types in a flow of evolutionary change. Two factors cause this change: chance and natural selection (Darwin 1859; Mayr 1983). An organism with a new genotype (a mutant) has to deal with a complex environment which is set by its competitors, the abiotic conditions and the food web context in which it lives. This ecological embedding will determine how density dependence limits population growth and will thus affect how natural selection acts on mutant features (Mylius 1999). If the mutant has a new feature that allows it to invade this complex environment, we may call this feature an 'adaptation' and say that the mutant has a higher fitness. Behavioural and evolutionary ecologists are interested in evaluating whether the features we observe in organisms today are adaptations. To infer whether a feature or a combination of features is the result of natural selection, instead of chance alone, we need to show that it actually would be favoured by selection (Mayr 1983).

The adaptive value of behaviour can readily be studied in insect parasitoids. In these animals foraging behaviour is closely linked with reproductive success (Cook & Hubbard 1977; van

Alphen & Vet 1986; Godfray 1994). We may ask whether the behavioural patterns we observe in these animals today consist of adaptations as a result of natural selection. It would be ideal if we would know the genes involved in foraging behaviour, their variability and correlations with the rest of the genotype, their effect on aspects of the phenotype other than foraging behaviour, and the details of their expression in relation to environmental conditions. Then we could study the link between gene frequencies and ecological interactions directly. Unfortunately, little if any such genetic information is currently available, although we may know more about parasitoid genome sequences and the expression of genes in the near future. Linking genetic and phenotypic approaches may currently not be workable or effective (Lessells 1991). Behavioural ecologists have not let themselves be discouraged by the above mentioned lack of information. They have decided to study questions on adaptation by focusing on the phenotype (e.g. foraging behaviour) while basically ignoring the mechanisms of genetics. Phenotypic modellers mainly rely on two approaches.

A game theoretic approach is adopted when the fitness of particular phenotypes depends on their frequency in the population (Maynard Smith 1982). It assumes that different types of behaviour (strategies) play against each other in an evolutionary game. The solution to this game is called the evolutionarily stable strategy (ESS). When almost all individuals in the population have the ESS phenotype, no alternative strategy can invade that population (Maynard Smith 1982, 1989; Marrow & Johnstone 1996).

When the fitness of particular phenotypes is not critically dependent on their frequency in the population, an optimisation approach can be adopted (but see Heino *et al.* 1998; Mylius 1999). Models are made in which the costs and benefits are evaluated of different types of behaviour (decisions), in terms of a chosen fitness criterion, and under certain constraints with respect to what can be decided or obtained. The 'best' or optimal decision within the context of the model is then compared to what the animal under study really does. This can suggest new hypotheses to be tested, and may thus lead to new insights. This approach has led to a body of theory called optimal foraging theory (Stephens & Krebs 1986).

Optimal foraging theory, and more in general the 'adaptationist programme' has received criticism, for several reasons. First of all, "breaking an organism into unitary traits and proposing an adaptive story for each considered separately" (Gould & Lewontin 1979) is an atomistic approach that would not do justice to the holistic nature of the genotype. Secondly, a characterisation of natural selection as a mechanism that produces perfection does not hit the mark, a point made with lavish rhetoric and ridicule by Gould & Lewontin (1979). Although correct, these points criticise a caricature of what the 'adaptationist programme' really is (Mayr 1983). Most adaptationists will agree that the process of natural selection is constrained in many ways.

However, developments in the field of long-term evolution have led to an idea that tries to circumvent the problem of genetic constraints. Peter Hammerstein's (1996) 'streetcar theory of evolution' supposes that although genetics does matter and is important in short-term evolution, long-term evolution may be relatively free of genetic constraints. Short-term evolution may lead to equilibria that do not match the 'phenotypic optimum'. However, according to the 'streetcar theory' new mutant alleles could destabilise such equilibria at a longer time scale, allowing further evolution. Thus the evolutionary course of the population can be compared to that of a streetcar, which repeatedly comes to a halt at temporary stops and starts moving after new passengers -new mutants- have entered it. This process would repeat itself until no new alleles are able to destabilise the equilibrium, at which time the tram would halt at its final stop (Hammerstein 1996). The population phenotypic strategy at this equilibrium is a Nash equilibrium (a best reply against itself, see Hofbauer & Sigmund 1988), and can be an ESS (Hammerstein & Selten 1994; Hammerstein 1996; Weissing 1996; Marrow & Johnstone 1996). Thus the end point of long-term evolution could coincide with predictions from phenotypic models. However, a change in that environment may open up the possibility for new mutants to invade and thus set the evolutionary streetcar going again (Hammerstein 1996). This last point is a reason for concern. The 'streetcar' theory only works when ecological embeddings remain fixed across evolutionary time scales. In nature, selection pressures may change frequently and radically long before the 'ESS' mutation has a chance to occur. For example, during the late Pleistocene, a mere 12,000 years ago, most modern ecological communities did not exist in their present locations, or consist of the particular mixture of species that coexist today (Futuyma 1986). This time scale problem suggests that the 'streetcar' idea does not solve the issue of genetic constraints. These and other constraints may be important most of the time and temporary local optima may be the norm in nature. The static idea of the 'streetcar' will not apply to behavioural traits that have evolved recently and to traits evolving under fluctuating selection (e.g. parasitoid-host coevolution) (Weissing 1996).

In this research project I have chosen not to contrast the foraging strategies of *Cotesia* parasitoids with an a priori 'phenotypic optimum'. In the absence of knowledge on genetic constraints I have approached constraints at the level of the phenotype and studied behavioural mechanisms and limitations experimentally. The results of such experiments have served as a context for my inferences on adaptation. I have used a detailed simulation model to extrapolate from observed foraging strategies to lifetime reproductive success in different environments and investigated the sensitivity of reproductive success to changes in these foraging strategies.

A pairwise comparative method

Interspecific and intraspecific variation in parasitoid foraging behaviour is evaluated, in relation to the spatial distribution of herbivorous hosts across plants. Differences between populations of one species or between pairs of species within the same genus reflect relatively recent evolutionary change ('short' term evolution). Making such comparisons offers several advantages. Adaptive differences between such groups do reflect responses to environmental variation, as ancestry does not play a role. After all, congeners and populations of the same species are likely to have an 'immediate' common ancestor, which makes differences in traits likely to actually reflect differentiation. Moreover, few variables are likely to confound the results of comparisons, simply because congeners and pairs of populations are similar in many aspects of their biology (Møller & Birkhead 1992). Furthermore, taxonomists agree more often on the taxonomy of closely related species than on distantly related ones, which reduces the problem of poorly known phylogenies when making comparisons (Møller & Birkhead 1992).

If one chooses to compare closely related groups that forage in habitats that are similar in all but one important aspect, then any observed adaptive variation is likely to be actually related to variation in that aspect of the environment. A combined analysis of congeners and populations may provide information on time scales of evolutionary change. The power of this approach is limited by the number of comparisons that can be made. If only a few populations are available for comparison, the results will mainly serve to suggest further hypotheses to be tested.

Host distributions and the value of information

Hosts will be under selection to occur in spatial distributions that minimise the chances of parasitism, while parasitoids are under selection to deal efficiently with present distributions of hosts across patches. Both hosts and parasitoids are small animals in a large world, and host location requires the use of different sensory modalities for orientation in spatially structured environments. Senses provide only local information. Hiding hosts may take advantage of sensory and other constraints in host-seeking parasitoids. This is another good reason to study constraints. They may play an interesting role in the evolutionary game between parasitoids and hosts.

Some of the early foraging models, e.g. the marginal value theorem (Charnov 1976) assumed that animals have 'complete information' on the distribution and density of resources in their environment, which is unlikely to be the case in nature. Equivalently, these models did not take into account that parasitoids may sample their environment (Cook & Hubbard 1977) and thus gain experience on which to base their foraging decisions. There is clear empirical evidence that experience affects parasitoid decisions on where to go and how long to stay (Papaj *et al.* 1994; Vet *et al.* 1995). These decisions are crucial for reproductive success and have been central to the average-rate maximising prey- and patch-models of early foraging theory (Stephens & Krebs 1986).

Many authors have set to study the mechanisms of patch use in a functional context (e.g. Waage 1979; Haccou *et al.* 1991; Hemerik *et al.* 1993; Driessen *et al.* 1995; Vos *et al.* 1998). These studies focused on the mechanisms employed by parasitoids to make decisions on how long to stay searching in patches with hosts. Two types of information emerged as key factors affecting parasitoid decisions on patch time allocation: the concentration of host-derived infochemicals in a patch and the timing of ovipositions. Parasitoids that are able to accurately estimate host density based on infochemical information may use this effectively to exploit hosts in any type of spatial distribution. In this case ovipositions provide reliable information on how many unparasitised hosts remain in the patch, as the initial density in the patch is known. Hosts will face difficulties to manipulate the efficiency of such parasitoids through their spatial distribution across patches.

On the other hand, when parasitoids are unable to make an accurate initial assessment of host density in a patch, hosts will have a wide scope for manipulating parasitoid efficiency through changes in host distribution. In this case only the timing of ovipositions can be used by the parasitoid, while the pay-off of different behavioural rules to deal with such information depends critically on the spatial distribution of hosts across patches (Iwasa *et al.* 1981). To give a simple example, if parasitoids currently have a tendency to stay a long time in a patch after a first oviposition, hosts 'should' occur singly in patches. All parasitoids will then waste a lot of their time and that will reduce the risk of parasitism.

However, if parasitoids currently have a high tendency to leave immediately after a first oviposition, then the sharing of patches by hosts would reduce the chances of parasitism. The concentration of infochemicals in a patch represents valuable information to parasitoids with the ability to use it for accurate assessment of host density, as this information allows them to adaptively change their behaviour. These same infochemicals are much less valuable to parasitoids that are unable to assess their concentration. This may be a general phenomenon. Information is only as valuable as it is useful to change behaviour (Stephens 1993).

The biology and spatial ecology of *Cotesia* parasitoids, *Pieris* herbivores and *Brassica* plants

Parasitoids

Cotesia glomerata (L.) lays clutches of eggs inside the caterpillars of several *Pieris* species, as it is a gregarious larval endoparasitoid (Laing & Levin 1982). The longevity of *C. glomerata* females in the field is unknown. In the laboratory females can live up to five weeks if fed with honeywater (Laing & Levin 1982). In a cage in the field female *C. glomerata* that were provided with a honey-solution and water lived up to four or five days (Geervliet 1997). *C. glomerata* females have between 500 and 2000 eggs upon emergence and can produce several hundred more during adulthood (Moiseeva 1976; Shapiro 1976; le Masurier & Waage 1993).

Cotesia rubecula lays single eggs, mainly inside *Pieris rapae* caterpillars, as it is a solitary larval endoparasitoid. In the laboratory females live between three and 26 days, with a mean of 17 days. In field cages *C. rubecula* female parasitoids lived on average 14 days (Geervliet 1997). *C. rubecula* females have around 30 eggs upon emergence and can produce between 40 and 80 more later in life (Nealis 1990).

Herbivore species and parasitoid development

C. glomerata 's main hosts in Europe are the large cabbage white, *Pieris brassicae* and the small cabbage white, *P. rapae*. When given a choice between these two hosts, *C. glomerata* prefers to oviposit in *P. brassicae* (E.A. van der Grift, M.P. Huiser & L.E.M. Vet unpublished). *P. brassicae* and *P. rapae* are both highly suitable for *C. glomerata* development (Brodeur *et al.* 1998), but *P. brassicae* sustains the development of larger clutches and larger wasps in a single larva (Harvey 2000).

P. rapae is more suitable for *C. rubecula* development than *P. brassicae,* as *P. brassicae* larvae parasitised by *C. rubecula* often die prematurely (Brodeur *et al.* 1998).

Host distributions in Europe

The basic egg-laying pattern of *P. rapae* results in a Poisson distribution of larvae across plants in Europe. Most infested plants have a single *P. rapae* larva. In contrast, *P. brassicae* occurs in aggregates of gregariously feeding caterpillars on leaves. Such clusters occur in variable sizes of up to 150 larvae across plants. Such clusters of *P. brassicae* are rare in most of the years in the Netherlands (Pak *et al.* 1989). The basic spatial pattern of these two *Pieris* caterpillars in Europe consists of few patches with many *P. brassicae*, and more patches with few *P. rapae*.

Host distributions in North America

P. rapae may have a Poisson or a somewhat more clumped negative binomial distribution across plants in North America, depending on the time in the growing season. In comparison with Europe, larger *P. rapae* population densities build up each year in North America. This results in many *P. rapae* patches with relatively high densities per patch. *P. brassicae* is absent in North America. There is no other gregariously feeding *Pieris* species on this continent.

Interspecific variation in foraging behaviour

The foraging behaviour exhibited by *C. glomerata* seems more adapted to the exploitation of gregarious *P. brassicae* larvae than of solitary *P. rapae* larvae (Wiskerke & Vet 1994). *C. glomerata* exhibits very rapid sequences of ovipositions within *P. brassicae* clusters, but needs a long time to find solitary larvae on *P. rapae*-infested leaves (Vos, re-analysis data Wiskerke & Vet 1994). *C. rubecula* is more efficient when foraging on *P. rapae* patches. We hypothesised that this difference was due to variation in walking patterns between the two parasitoid species (with *C. glomerata* wasting time due to area restricted search near solitary hosts). However, analysis of search tracks with an EthoVision video tracking system showed indistinguishable search patterns. The only significant behavioural difference in intrapatch behaviour was a higher walking speed in *C. rubecula* that causes it to encounter hosts at a higher rate (Vos unpublished).

Plants

About 100 species of Cruciferae are known as host plants of *P. brassicae*, *P. rapae* and *P. napi* (Geervliet 1997). These comprise both wild crucifers and cultivated crop plants like cabbages. A preliminary study showed that cultivated cabbages, especially Brussels sprouts plants (*Brassica oleracea gemmifera*) were most attractive to *Pieris* herbivores in a field with 13 species of wild and cultivated crucifers (L. Castricum, J.J.A van Loon & M. Vos unpublished). Herbivore-infested cabbages are also highly attractive to *Cotesia* parasitoids (Geervliet *et al.* 1996). The *Pieris-Cotesia* system may originally have evolved on small wild crucifers, but cabbages represent a much higher nutritional value, and attraction to these larger plants is not surprising. Wild crucifers may still be important early in each season when cultivated cabbages are not yet available.

For this research project we used Brussels sprouts plants (*B. oleracea gemmifera* cv Icarus), both in the laboratory experiments and in the field. Plants were about 40 cm high in the laboratory and had around 16 leaves. In the field the plants could grow to become 1 m tall and could have around 40 leaves with a diameter of up to 40 cm. The plants in the field and in the laboratory semi-field environments were set up as monocultures. Thus parasitoid interplant travels were always between *B. oleracea* plants.

The community

An entire community of herbivore species occurs on cabbages, including aphids, several caterpillars, *Phyllotreta* beetles, leaf miners and root flies (Kirk 1992). All these herbivores may affect the production of plant volatiles and thus affect the interaction between *Pieris* hosts and *Cotesia* parasitoids. This implies that the spatial distribution of nonhosts may be as important to parasitoid foraging strategies as the distribution of hosts.

RESEARCH OBJECTIVES

I explored the strategies of parasitoids that forage for host species with different spatial distributions across plants. Firstly, I investigated interspecific variation in the patch exploitation mechanisms of *C. rubecula* and *C. glomerata* that forage in the same habitat with cruciferous plants, but prefer hosts with different spatial distributions. Secondly I evaluated whether adaptive intraspecific variation in foraging behaviour could be inferred between *C. glomerata* populations that have experienced different host distributions for about 350 generations. Throughout this thesis I investigated both constraints and plasticity in parasitoid responses to information from herbivores and plants. A third objective was to investigate the effects of variation in information use by parasitoids at the level of the community. The general aim is to understand the evolution and spatial ecology of parasitoid-host interactions and information use in this tritrophic system.

Interspecific variation in patch exploitation

The first objective was to compare the foraging behaviour of two closely related parasitoid species (*C. rubecula* and *C. glomerata*) with respect to leaving tendencies from patches in different semi-field environments. Parasitoids are unlikely to have complete information on the quality of their habitat, but they may acquire local information and experience. Parasitoids clearly increase their foraging effort in microhabitats where they had rewarding experiences like successful ovipositions (Papaj *et al.* 1994). However, it is not always obvious whether rewarding experiences should increase or decrease the animal's leaving tendency: in some patch types (e.g. when there is generally only a single host present) it is adaptive to leave directly after an oviposition (Strand & Vinson 1982), while in others it is better to stay.

In **Chapter 2** I clarified this issue for the *Cotesia-Pieris* system and investigated how intrapatch experiences like contact with feeding damage and encounters with solitary or clustered hosts influence parasitoid patch leaving decisions. I also investigated the effect of experiences in previously visited patches on foraging decisions in the present patch. I chose a statistical modelling approach to dissect the behavioural strategies of these parasitoids, using the proportional hazards model (Cox 1972). This method allows inferring whether the parasitoids use simple fixed rules or make complex flexible decisions. In addition I compared patch exploitation in these *Cotesia* parasitoids with the mechanisms that have been proposed by Waage (1979) and Driessen *et al.* (1995) for the parasitoid *Venturia canescens*. Contrasting different parasitoid-host systems may help us to take a step beyond system-specific ecology.

Intraspecific variation between *Cotesia glomerata* populations

The second objective was to investigate intraspecific variation between different *C. glomerata* populations. A classical biological control program provided a unique opportunity to test ecological and evolutionary hypotheses in this system (see le Masurier & Waage 1993). The parasitoid *C. glomerata* was introduced from Britain to the USA in 1884 to control the lepidopterous pest *P. rapae* (Clausen 1956). *P. brassicae* is absent in the USA, which forces North American *C. glomerata* to deal with solitarily feeding hosts. European *C. glomerata* have to decide whether they will actually accept the *P. rapae* larvae they are more likely to encounter, or whether they will reject these as a host, to spare eggs for a possible 'jackpot' cluster of *P. brassicae* larvae. It may not be adaptive to use a fixed decision rule like 'only accept *P. brassicae*'. Instead, female parasitoids may use various cues for the presence or absence of *P. brassicae* in the current environment.

Le Masurier and Waage (1993) have shown that more than 100 years after their introduction, *C. glomerata* from the USA have a higher attack rate on *P. rapae* than British *C. glomerata.* These results did not provide any clue as to which aspects of parasitoid behaviour might be different between American and British strains of *C. glomerata.* North American parasitoids might have evolved new traits for the exploitation of *P. rapae*, or have lost some characteristics of their behaviour that are especially tuned to foraging for highly clustered *P. brassicae.* Both scenarios might result in an increased efficiency on the solitary host.

One important aspect of parasitoid behaviour, that may affect attack rates, is host acceptance. In **Chapter 3** I investigated whether differences in host acceptance between the different strains of *C. glomerata* could explain the higher rate of attack as observed by le Masurier & Waage (1993). Furthermore I studied whether the host species in which a parasitoid develops has a phenotypic effect on host acceptance in the adult animal. Host-derived information perceived during development or emergence might be a cue for European *C. glomerata* to the presence or absence of *P. brassicae* in its environment. In addition I examined the effect of oviposition experiences in *P. brassicae* versus *P. rapae* on subsequent host acceptance of *P. rapae.* For the pairwise comparison between parasitoid populations I used *C. glomerata* strains that had both been reared on *P. rapae.*

The experiments by le Masurier & Waage (1993) have suggested that *C. glomerata* has adapted to attack *P. rapae* in North America. One of the limitations of that study was the confinement of tested parasitoids to cages. Since I was interested in the possibility of adaptation to spatial distributions of hosts, I used behavioural observations in semi-field set-ups, thus allowing the parasitoids to travel between plants and leaves infested with hosts.

In **Chapter 4** I investigated travel patterns in *C. glomerata* strains from Europe and North America, focusing on tendencies to make explorative flights and to travel between and within plants. I examined patch leaving and arrival at the levels of plants and leaves and measured travel times between patches. Travel times are important in determining the adaptive value of patch leaving decisions (see e.g. Driessen & Bernstein 1999). Accurate estimates of parasitoid travel times are scarce in the literature (but see e.g. Völkl 1994; Völkl & Kraus 1996). To understand patch exploitation in parasitoids, it is essential to know whether parasitoids make decisions based on local information from the present patch, or use information from other patches in the environment while exploiting the current patch. Therefore I also studied whether the parasitoids used olfactory information from an alternative, nearby patch of much higher quality, to make patch leaving decisions on the current patch.

In **Chapter 5** I used the behavioural data from my semi-field environments to parameterise a simulation model of *Cotesia glomerata* foraging behaviour in a large field with *Brassica* plants. The general aim was to relate the variation in foraging behaviour between American and European parasitoids to variation in lifetime reproductive success. The performance was investigated of both foraging strategies on the different host distributions occurring in North America and Europe. Furthermore I checked how robust these strategies are to the ability or inability of parasitoids to assess host density on plants and leaves. I examined whether the foraging strategy of the American population is more successful in the North American environment than the European strategy, 350 generations after *C. glomerata*'s introduction to North America. Furthermore I considered host decisions on how to distribute offspring across leaves. Could the host manipulate parasitisation rates by North American parasitoids by changing the distribution pattern of its offspring? I asked to which aspects of parasitoid behaviour lifetime reproductive success is most sensitive and investigated the proportion of time limitation in European and American parasitoid populations in environments with different host distributions. The proportion of time limitation in a population indicates how natural selection will act on parasitoid behaviour. If most parasitoids die before they have laid all their eggs, and are thus time limited, natural selection is likely to act on host encounter rates.

Hide-and-seek on entangled banks

Infochemicals play a key role in multitrophic relationships, mediating direct and indirect interactions (Vet & Dicke 1992; Dicke &Vet 1999; Stowe *et al.* 1995; Sabelis *et al.* 1999). The information web, based on infochemicals, is more complex than the food web (Dicke & Vet 1999; Vet 1999). Any infochemical can potentially be used in the battle between consumers and resources, either for defences, or for attacks. Many parasitoids and predators of insect herbivores use volatiles from herbivore-infested plants for the long-distance location of their victims (Vet & Dicke 1992). The majority of plant species in the field will be attacked by a complex of herbivores (Lawton & Schröder 1978; Futuyma & Gould 1979; Futuyma 1983). Natural enemies will have to deal with this complexity. This is the topic of **Chapter 6**. As yet there are no studies available on the volatile blends produced by plants infested with a complex of herbivore species. It is likely though that such blends are more difficult to 'interpret' for natural enemies.

Recent advances in the diversity-stability debate have not taken into account that many trophic interactions are mediated by infochemicals (e.g. McCann *et al.* 1998; see McCann 2000 for a review; Borrvall *et al.* 2000). These studies show that species diversity can increase food web stability, when weak trophic links dampen the oscillations of strong consumer-resource interactions (McCann *et al.* 1998; McCann 2000). Smaller fluctuations reduce the probability of extinctions, thus promoting food web persistence. I studied the effect of herbivore diversity on the use of plant information by parasitoids. Is plant information less informative in a multiple-herbivore environment, and does this weaken potentially strong parasitoid-host interactions? Field data were examined with respect to herbivore species diversity on the single plant species *B. oleracea*. In laboratory experiments I investigated whether parasitoids are constrained in their ability to discriminate between leaves infested with hosts, non-hosts, and complexes of host and non-host herbivores. Based on the results models were explored of parasitoid-herbivore communities that occur on a single plant species. I studied the effect of information links on trophic links, which is qualitatively different from a weak trophic interaction dampening a strong one (McCann *et al.* 1998). I hypothesised that small increases in diversity at the herbivore level will increase the persistence of the parasitoid community and that extinctions are to be expected at high levels of herbivore diversity.

In addition the different parasitoid species in the model were allowed to be affected in varying degrees by non-host herbivores to study the effects on the community.

In this project I aimed to partly disentangle the information web, on an entangled bank clothed with crucifers, with various butterflies and parasitoids flitting about, and to relate differences in their behaviour to lifetime reproductive success and the persistence of the community.

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Patch exploitation by the parasitoids *Cotesia rubecula* and *Cotesia glomerata* in multi-patch environments with different host distributions

Summary

We analysed the foraging behaviour of two closely related parasitoid species (*Cotesia rubecula* and *Cotesia glomerata*) with respect to leaving tendencies from patches in different environments. We investigated how intrapatch experiences like contact with feeding damage and encounters with hosts influence patch leaving decisions. We also estimated the effect of experiences in previously visited patches on leaving decisions in the present patch.

For this analysis we applied the proportional hazards model (Cox 1972) to data collected in three versions of a multiple patch set-up. These set-ups consisted of different host species or combinations of host species: (1) *Pieris rapae*, (2) *Pieris brassicae*, (3) both *P. rapae* and *P. brassicae*. The larvae of these hosts differ in their spatial distribution on plants: *P. brassicae* occur in clusters and the distribution of larvae is heterogeneous; *P. rapae* larvae feed solitarily.

The specialist parasitoid *C. rubecula* used a simple strategy: highest leaving tendency on empty leaves, lower leaving tendency on leaves infested with the non-preferred host *P. brassicae*, lowest leaving tendency on leaves infested with the preferred host, *P. rapae*. In the environment with both host species, the leaving tendency only decreased on leaves infested with *P. rapae*. The generalist *C. glomerata* used a more complex set of rules: (a) Multiple ovipositions on the present patch decreased the leaving tendency on leaves containing the gregarious host. (b) Once the parasitoid had encountered two or more hosts, it had a lower leaving tendency during subsequent patch visits. (c) The leaving tendency increased with the number of visits on infested leaves. In environments where the less preferred host *P. rapae* was present, *C. glomerata* switched to the same simple type of rule as used by *C. rubecula*.

Neither of the two *Cotesia* species used a count-down rule, in which ovipositions increase the leaving tendency. We discuss how patch exploitation by both *Cotesia* species compares to the patch exploitation mechanisms as proposed by Waage (1979) and Driessen *et al.* (1995).
We formulate an '*adjustable termination rate*' model for patch exploitation in both *Cotesia* species in multi-patch environments.

INTRODUCTION

Optimal foraging theory attempts to relate variation in reproductive success of individuals to variation in their foraging behaviour. Several optimality models have focused on behavioural decision variables such as patch residence time. The marginal value theorem (Charnov 1976) considers the optimal residence time in a patch and suggests that this depends on the gain in the patch, travel times and the rate of gain in the habitat averaged over the total time spent there. Charnov's model assumes that the animal has 'complete information', which is unlikely to be the case in nature. His model does not suggest a mechanism or decision rule that foraging animals could apply to achieve the optimal residence time.

This generates the question how animals should make decisions on when to leave a patch? Several authors have considered what mechanisms might be employed to achieve optimal patch residence times. It was suggested that animals use simple, rather fixed 'rules of thumb' (see Cowie & Krebs 1979; Stephens & Krebs 1986). A number of analyses focused on the performance of such simple patch leaving rules (Iwasa, Higashi & Yamamura 1981; McNair 1982; Green 1984). However, experimental evidence for the general use of such simple decision rules is scarce. If animals have incomplete information on patch and habitat profitability, learning through experience and sampling may provide a mechanism for the optimization of patch leaving decisions. There is clear empirical evidence that experience affects parasitoid decisions on where to go and how long to stay (Papaj *et al.* 1994; Vet, Lewis & Cardé 1995). Animals can increase their foraging effort in microhabitats where they had rewarding experiences, like successful ovipositions, through associative learning (Papaj *et al.* 1994). However, it is not always obvious whether rewarding experiences should increase or decrease the animal's leaving tendency: in some patch types (e.g. when there is generally only a single host present) it is adaptive to leave after one oviposition (Strand & Vinson 1982), while in others it is better to stay.

This leads to the question what kind of cues animals could use to achieve adaptive patch residence times. Waage (1979) used a parasitoid as a model system and proposed a patch exploitation mechanism for *Venturia canescens*: when a parasitoid enters a patch it has a tendency to stay in that patch and to turn around when encountering the edge of the patch. This responsiveness to the patch edge is initially set by the intensity of the host-associated chemicals (kairomones) in the patch. With time, this responsiveness decays at a constant rate to a specific threshold, after which the parasitoid leaves the patch. Ovipositions increase the responsiveness, thereby *increasing* patch residence time. In a recent study Driessen *et al.* (1995) proposed a decision mechanism for patch leaving in the same species that contrasted to that of Waage (1979) in one important way: after the initial assessment of host density, ovipositions decrease the responsiveness, thereby *decreasing* patch residence time (a count-down mechanism). The most important factor determining which mechanism is adaptive, is the accuracy of patch density assessment. If this is accurate, the count-down mechanism is adaptive. The second factor differentiating between these rules is host distribution and depends on the first factor. In an environment where patches contain a uniform number of hosts (and patch assessment is accurate), a count-down rule may perform most efficiently, while in a habitat with a heterogeneous host distribution (and inaccurate patch assessment) Waage's mechanism might be adaptive.

In the patch exploitation mechanisms as proposed by Waage (1979) and Driessen *et al.* (1995) only intra-patch factors play a role. However, the marginal value theorem assumes that the response to patches is tuned to mean host availability in the environment. Hence, it is essential to consider whether patch leaving decisions change as the parasitoid gains experience about the world in which it lives. To answer this question, it is important to observe the animal in an environment that allows it to express its entire range of natural behaviour, i.e. in a multiple patch environment in which the animal has a place to go to after leaving the patch.

Several authors have correlated patch leaving decisions to experiences on the current patch by means of the proportional hazards model (Cox 1972). Hemerik *et al.* (1993) and Haccou *et al.* (1991) showed that the leaving tendency of two *Leptopilina* parasitoid species decreased with the presence of kairomone, ovipositions and high recent oviposition rates. Van Roermund *et al.* (1994) showed that the presence of honeydew and ovipositions decreased the leaving tendency of the parasitoid *Encarsia formosa*. Van Steenis *et al.* (1996) showed that the leaving tendency of

Aphidius colemani only decreased at patches containing a high density of 100 hosts. On these patches *A. colemani* used a count-down mechanism: ovipositions increased the leaving tendency, especially after the parasitoids had encountered 100 hosts or more.

Time allocation to foraging behaviour should be adapted to the density and spatial distribution of hosts in patches. Hosts may occur singly, evenly distributed or clustered in a patch. Parasitoids that attack several host species differing in their spatial distribution may have evolved flexible patch leaving strategies. In the tritrophic system of crucifers, *Pieris*, and *Cotesia*, the host species differ markedly in their spatial distribution on the scale of plants and leaves. The small white butterfly (*Pieris rapae* (L.)) lays its eggs separately, often only one or a few on a leaf. This results in a rather low variance in the number of larvae per leaf. The larvae are also evenly distributed over a leaf. We will call this the 'uniform' distribution. The large white butterfly (*Pieris brassicae* (L.)) lays its eggs in clusters of seven to 150 eggs, so young larvae have a more heterogeneous distribution. *Cotesia glomerata* (L.) is a gregarious larval endoparasitoid of several *Pieris* species (Brodeur, Geervliet & Vet 1996). It attacks both *P. brassicae* and *P. rapae*, with a higher acceptance of *P. brassicae* larvae. First and second instar *P. rapae* larvae are readily accepted (Brodeur *et al.* 1996). The solitary larval endoparasitoid *Cotesia rubecula* (Marshall) is a specialist on *P. rapae*, but it will accept *P. brassicae* larvae as well (Brodeur *et al.* 1996). Hence, *C. glomerata* has to deal with host species that occur in uniform as well as heterogeneous distributions, while *C. rubecula* is specialized on the uniform host distribution of *P. rapae*. To both *Cotesia* species there is a clear advantage in developing in the preferred host species (Geervliet & Brodeur 1992). Naive females of both *C. glomerata* and *C. rubecula* do not discriminate between infochemicals from plants infested by *P. rapae* and *P. brassicae* (Geervliet, Vet & Dicke 1994). There is evidence that both parasitoid species visit both patch types in the field (Geervliet *et al.* 2000).

Using the *Cotesia-Pieris* system, we specifically address the following questions:

1) Do *C. glomerata* and *C. rubecula* show differences in the way they use information to make patch leaving decisions?

2) Do both *Cotesia* species alter their patch leaving strategies in environments that differ in the available host species?

3) Do the parasitoids use simple rules of thumb, or do they employ complex, flexible rules?

4) Do the parasitoids use Waage's (1979) patch exploitation mechanism on the host with the heterogeneous distribution and Driessen *et al.*'s (1995) count-down mechanism on the uniformly distributed host?

METHODS

Experiments

In our analysis we used the behavioural data collected by Wiskerke & Vet (1994). We summarize their methods below. Full details of the experimental procedure are given in their paper. The foraging behaviour of *C. rubecula* and *C. glomerata* parasitoids was observed in a 'semi-field set-up' with *Pieris*-infested cabbage plants in a greenhouse compartment. Eight Brussels sprout plants were placed on a table in two parallel rows. Four of these plants were clean, while the other four were infested. Two fans placed at the end of the table provided an air stream of 0.3-0.4 $m \cdot s^{-1}$ at the parasitoid release site. This release site, situated at the downwind end of the table, consisted of an excised Brussels sprouts leaf with feeding damage (no hosts), inflicted by the same species of host(s) as present in the particular experiment. The leaves had a diameter of about 12 cm. Three types of experiments per parasitoid species were conducted. In these, eight plants were used in the following combinations: (I) four plants infested with *P. brassicae* larvae and four clean plants; (II) four plants infested with *P. rapae* larvae and four clean plants and (III) two plants infested with *P. rapae* larvae, two with *P. brassicae* larvae and four clean plants. Butterflies of each *Pieris* species were allowed to oviposit on the respective experimental plants. The excess of eggs was removed to produce the desired experimental density. A plant infested with *P. brassicae* contained on average 20 early first instar larvae (hereafter EL1), in one or two clusters. The density in such clusters ranged from one to 30. A plant infested with *P. rapae* contained 20 larvae as well, but more evenly distributed over several leaves on the plant. Each infested leaf contained 1-8 solitarily feeding EL1 larvae (average 2.44, s.d. 1.34). The foraging behaviour of individual parasitoids (*C. rubecula* or *C. glomerata*) was observed and recorded continuously. Each observation started at the moment the parasitoid left the release site and flew to a plant. An observation was terminated after one hour or when the parasitoid left the foraging arena, landed elsewhere and remained there for more than one minute (Wiskerke & Vet 1994). For each treatment 18 to 24 females of each *Cotesia* species were tested.

The proportional hazards model

Here we give a short explanation of the essentials of the model, for a more thorough description we refer to Kalbfleisch & Prentice (1980) and Haccou & Hemerik (1985). The proportional hazards model is used to analyse which factors in the environment (or experiences of the parasitoid) are correlated with an increase or decrease in the tendency of a parasitoid to leave a patch. It is assumed that the parasitoids have a basic tendency to leave the patch (base line hazard), which is reset after certain events, so-called renewal points. Renewal points occur here at the moment a patch is entered and when searching resumes after an oviposition. The model is a multiple regression method, with the relative strength of each of *p* factors being estimated by means of partial likelihood maximization (see Kalbfleisch & Prentice 1980).

Equation 1 describes the effect of those factors on the leaving tendency:

$$h(t;z) = h_0(t)\exp\{\sum_{i=1}^{p} \beta_i z_i\} \qquad \text{eqn 1}$$

in which $h(t;z)$ is the probability per second to leave the patch (in our case when the parasitoid flies away from the leaf), and $h_0(t)$ is the basic tendency to leave, i.e. when there is no effect of any factor like experience or environmental information. The z_i are the factors (covariates) that might influence the leaving tendency. Each factor z can have different values e.g.: 'no host and feeding damage present' would be represented by 0, while the presence of the host and feeding damage would be coded by 1. The β values are the relative strengths of the effects of the covariates. These are estimated in the analysis. The influence of experiences (the covariates) on the leaving tendency is modelled as a multiplicative effect of $\exp(\beta_i z_i)$ on the base-line hazard. If this term is below one, the leaving tendency is reduced, above one it is increased. An increased leaving tendency implies a shorter giving up time (GUT). The expected GUT is $1/h(t;z)$.

Covariates

The selection of covariates is a crucial step in the analysis. Many factors may have could be an effect on the parasitoids' leaving tendency. We have taken into account the biology of both *Cotesia* parasitoids, factors found to be important in other parasitoids and some factors generally presumed to be important in patch leaving models. Factors including host-induced damage, kairomone concentration and ovipositions emerge as important in the foraging process. These factors have a high informational value and are reliable cues. We also allow for the use of experiences acquired during previous patch visits. It is important at which spatial scale we define the patch that is left. Depending on the behaviour of the animal, it might be the host, the spot with feeding damage and kairomones, a leaf or the plant. The parasitoids do not walk from leaf to leaf when searching for hosts on a plant. Movement from leaf to leaf is facilitated by flight. The most dramatic change in foraging behaviour occurs on leaves containing larvae and feeding damage (Wiskerke & Vet 1994). Therefore, we define the patch to be a leaf in our analysis. Hence, leaves that do not contain hosts and damage are empty patches. We define 'leaving' as flying away from a leaf, followed by landing somewhere else (e.g. another leaf). If the parasitoid takes off and subsequently relands on that same leaf, we consider this to be part of the same patch visit. These short excursions are rather similar to those of *Venturia canescens* as found by Waage (1979) and Driessen *et al.* (1995). We have chosen a leaving criterion that allows for a clear biological interpretation and is not as arbitrary as the '14 or 60 seconds off patch'-criteria of Waage (1979). An encounter with a host is defined by an ovipositor insertion into a host. From the behaviourial records of Wiskerke & Vet (1994) it was not possible to discriminate parasitism from superparasitism for both species of *Cotesia*. The description of the covariates we have selected, and the way they are coded, are given in Table 1.

Table 1 Covariates tested for having an effect on the leaving tendency.

1. The present leaf contains *P. brassicae* and host-damage (no/yes)=(0/1)
2. The present leaf contains *P. rapae* and host-damage (no/yes)=(0/1)
3. The number of encounters, i.e. ovipositor insertions, during the present leaf-visit (notation for 0, 1, 2 or more insertions is (0/1/$\geq$2) and it is coded as (0/1/2)
4. The total number of encounters in the protocol (0/1/$\geq$2)=(0/1/2)
5. The number of ovipositor insertions during the previous leaf-visit (0/1)=($\leq$1 and $\geq$2)
6. *P. brassicae* and host damage were present during the previous leaf-visit (no/yes)=(0/1)
7. *P. rapae* and host damage were present during the previous leaf-visit (no/yes)=(0/1)
8. The cumulative number of host-damaged leaves visited (0/1/$\geq$2)=(0/1/2)
9. The number of undamaged leaves visited since the latest ovipositor insertion (0/$\geq$1)
10. The time since the start of the behavioural observation

Statistical analysis

The experiments of Wiskerke & Vet (1994) resulted in six data sets. We analysed each data set by means of the proportional hazards model. After the likelihood maximization, our first step was to test whether the joint effect of all covariates was significant. Under the null-hypothesis $\beta_1=\ldots=\beta_p=0$, none of the covariates z_i has any effect on the leaving tendency. The test statistic T has asymptotically a Chi-squared distribution with p degrees of freedom (Miller 1981; Haccou & Hemerik 1985). The second step was to test for each β (and therefore each covariate) separately whether it had a significant effect. The third step was to test for pairwise effects of covariates that were not significant by themselves. When there are e.g. eight degrees of freedom, test statistics in the interval (3.84, 15.5) are not significant by themselves, but together with another covariate they can have a significant multiplied effect ($T>15.5$). We applied multiple comparisons to test for such pairwise effects. We chose to only consider single covariates and pairs of them because they allow for clear biological interpretations.

In addition to the proportional hazards analysis, we analysed part of the data with tests as used by Waage (1979) and Driessen *et al.* (1995). Waage's mechanism (1979) and Driessen *et al*'s count-down mechanism (1995) clearly contrast in the way ovipositions affect the residence time in a patch. However, the two mechanisms do not contrast as clearly with respect to the effect of an oviposition on the leaving tendency (see Figure 1).

Hence, separate tests were conducted for the effect of encounters on patch residence times. This makes comparisons more straightforward and serves as an extra check on the results of the model analysis. In these analyses we used all visits to leaves that the parasitoid had not visited before (the first visits to patches).

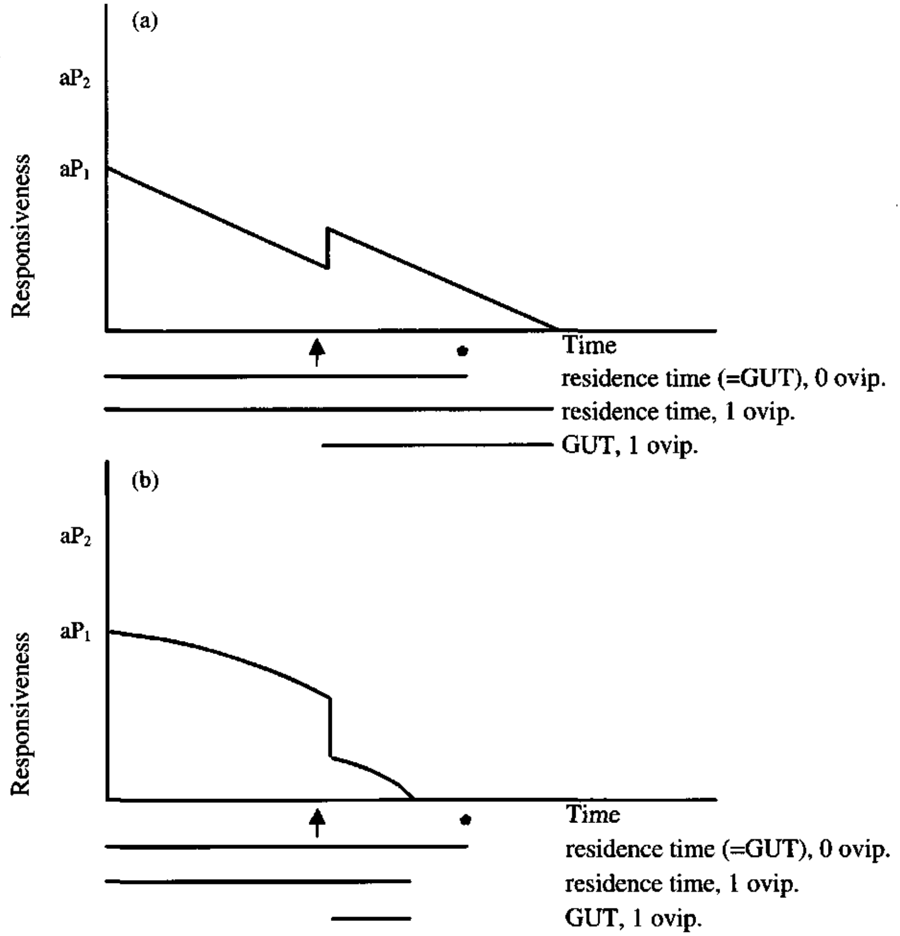

Figure 1 Simplified graphical representation of Waage's (1979) patch time model (a) and the count-down mechanism (Driessen *et al.* 1995) (b). The arrow marks the occurrence of an oviposition. If no oviposition occurs, the patch should have been left at the time indicated by the asterisk. Underneath the graphs the residence time and GUT of a patch visit in which one oviposition occurred, are compared to that of a patch visit in which no oviposition occurred. It should be noted that in both models the intercept of the line increases with host infestation.

RESULTS

Foraging behaviour

Wiskerke and Vet (1994) give an elaborate description of the foraging behaviour of both *Cotesia* species in the different environments. After taking off from the release site the parasitoids often flew to an infested plant and hovered over the leaves at a distance of a few centimetres. Most parasitoids visited several leaves on different plants. Both *Cotesia* species frequently made short excursions. Either they hovered over other areas of the same leaf, or they even flew over other leaves before relanding.

Baseline hazards

The estimated baseline hazards of *C. rubecula* and *C. glomerata* in the three different environments are given in Table 2. The basic leaving tendencies of *C. rubecula* and *C. glomerata* are high in the set-up where only their less preferred host was present, *P. brassicae* and *P. rapae* respectively. When we compare the estimated baseline hazards for both *Cotesia* species, it is clear that *C. rubecula* tends to have a higher leaving tendency than *C. glomerata* in all of the three environments.

Table 2 Estimated baseline hazards (probability per second to fly away) for *C. rubecula* and *C. glomerata* in the different environments.

Set-up	*C. rubecula*	*C. glomerata*
P. rapae	0.009749	0.004175
P. brassicae	0.01678	0.002410
Both *Pieris* spp.	0.008261	0.004501

Leaving tendency of *C. rubecula*

The combined effect of all covariates was significant in each of the three experiments ($p<0.05$, Table 3). *C. rubecula* used the same cue in all three environments: on leaves containing hosts and feeding damage the leaving tendency decreased (Table 4). In the environment with *P. rapae* this resulted in an increase in the expected GUT ($1/h(t;z)$) from 103 seconds on an empty leaf, to 237 seconds on an infested leaf. In the environment with *P. brassicae* the expected GUT increased from 60 to 102 seconds. In the environment with both *Pieris* species the leaving tendency only decreased on leaves containing the preferred host, *P. rapae*. The expected GUT increased from 121 seconds on a leaf that was clean or infested with the less preferred host *P. brassicae*, to 401 seconds on a patch with *P. rapae*. *C. rubecula* rarely stayed the complete one hour observation period in the set-up with *P. brassicae*. The parasitoids often flew to the roof of the glasshouse after about 30 minutes. *C. rubecula* employed a simple rule in all three environments, using information on the current patch to make patch leaving decisions.

Table 3 The value of the test statistic *T* (d.f.) for the Combined effects of all covariates on the leaving tendency in experiments with *C. rubecula*.

Set-up	*T*	(d.f.)
C. rubecula on *P. rapae*	71.06	(8)*
C. rubecula on *P. brassicae*	39.35	(8)*
C. rubecula on both *Pieris* spp.	124.94	(10)*

*P << 0.001.

Table 4 Covariates for *C. rubecula* (numbers as in Table 1). Test statistic *T* is marked with an asterisk if a covariate (or pair of covariates) has a significant effect. Downward arrows indicate a decreasing effect of a covariate on the leaving tendency.

Host(s)	Covariates	*T* (d.f.)	Effect on leaving tendency	β
P. rapae	(2) present leaf contains *P. rapae* and damage	43.77 (8)**	↓	–0.8385
P. brassicae	(1) present leaf contains *P. brassicae* and damage	21.03 (8)*	↓	–0.5384
Both spp.	(2) present leaf contains *P. rapae* and damage	85.26 (10)**	↓	–1.198

* P < 0.01; ** P < 0.001.

Leaving tendency of *C. glomerata*

The combined effect of all covariates was significant in all three experiments (Table 5). *C. glomerata* used information on the presence of hosts and feeding damage in all three environments: On infested leaves the leaving tendency decreased (Table 6). In the environment with *P. rapae* this resulted in an increase in the expected GUT from 240 seconds on an empty leaf, to 484 seconds on an infested leaf. In the environment with *P. brassicae* the expected GUT increased from 415 to 1021 seconds. In the environment with both *Pieris* species the increase was from 222 seconds on an empty patch to 499 seconds on a patch with *P. rapae* and 779 seconds on a patch with *P. brassicae*. In the set-up where *P. brassicae* was present, encounters with hosts on the present patch decreased the leaving tendency even further although its effect was only significant in combination with other covariates (Table 6).

Table 5 The value of the test statistic *T* (d.f.) for the combined effects of all covariates on the leaving tendency in experiments with *C. glomerata*.

Set-up	*T*	(d.f.)
C. glomerata on *P. brassicae*	140·94	(8)*
C. glomerata on *P. rapae*	27·22	(8)*
C. glomerata on both *Pieris* spp.	82.10	(10)*

* P < 0.001.

After multiple encounters the parasitoids stayed on average 2550 seconds. In the *P. brassicae*-environment experience acquired during previous patch visits influenced the leaving tendency. Three factors had a pairwise effect in combination with the number of encounters on the present patch: (i) the total number of encounters with hosts; (ii) the total number of infested leaves already visited; and (iii) the time in the protocol. The first decreased the leaving tendency, the second increased it, while the third had a decreasing effect. The total number of encounters with hosts and the time in the protocol had a pairwise decreasing effect on the leaving tendency. *C. glomerata* used a complex rule in an environment where only the gregarious host *P. brassicae* was present. In environments with the solitary host it switched to a simple rule in which the leaving tendency was mainly affected by the presence and type of infestation.

Table 6 Covariates for *C. glomerata* (numbers as in Table 1). Test statistic *T* is marked with an asterisk if a covariate (or pair of covariates) has a significant effect. Downward arrows indicate a decreasing effect, upward arrows an increasing effect of a covariate on the leaving tendency.

Host(s)	Covariates	*T* (d.f.)	Effect on leaving tendency	β
P. brassicae	(1) present leaf contains *P. rapae* and damage	16.34 (8)*	↓	−0.9003
	(3) # encounters on the present leaf	14.86 (8) NS	↓	−0.5573
	(4) total # encounters with hosts	5.96 (8) NS	↓	−0.3644
	(8) total # infested leafs visited	7.80 (8) NS	↑	0.4640
	(10) the time since start of observation	6.66 (8) NS	↓	−0.0003096
	3 & 4	28.67 (8)***		
	3 & 8	27.79 (8)***		
	3 & 10	23.83 (8)**		
	4 & 10	20.43 (8)**		
P. rapae	(2) present leaf contains *P. rapae* and damage	15.56 (8)*	↓	−0.7038
Both host spp.	(1) present leaf contains *P. brassicae* and damage	21.67 (10)*	↓	−1.254
	(2) present leaf contains *P. rapae* and damage	27.30 (10)**	↓	−0.8082

* P < 0.05; ** P < 0.01; *** P < 0.001; NS, not significant.

The effect of host distribution and density

Leaves infested with one cluster of *P. brassicae* larvae usually contained one large site with feeding damage. In contrast, leaves infested with low densities of *P. rapae* larvae usually contained several little sites with feeding damage. Both *Cotesia* species clearly distinguished the type of damage: *C. glomerata* had a high leaving tendency on the low density *P. rapae* patches and a lower leaving tendency on the high density *P. brassicae* patches. *C. rubecula* had a high leaving tendency on the high density *P. brassicae* patches and a low leaving tendency on the comparatively low density *P. rapae* patches. Apparently, for *C. rubecula* a high density does not automatically translate into a low leaving tendency. This excited our interest in the effect of larval density (and the corresponding level of feeding damage) on the leaving tendencies of both *Cotesia* species on patches with *P. rapae*. Analysis of leaving tendencies on patches containing one, two, three and four or more *P. rapae* larvae for visits in which no host encounters occurred, revealed that there was no significant effect of density on the leaving tendency, neither for *C. rubecula* (P=0.13, logrank test for survival curves), nor for *C. glomerata* (P=0.34, logrank test). Hence, larval density on *P. rapae*-infested leaves did not influence the leaving tendency in the parasitoids. However, the parasitoids do respond differently to clean and host-infested leaves and significantly stay longer on the latter (*C. rubecula*: $P=5\cdot3\times10^{-5}$, logrank test, $N_{empty}=50$, $N_{infested}=176$); *C. glomerata*: P=0.029, logrank test, $N_{empty}=48$, $N_{infested}=108$).

For *C. rubecula* there was a significant effect of encounters (0, 1, 2) on the residence time in patches infested with *P. rapae* ($P << 10^{-6}$, Kruskal-Wallis test; all pairs of groups are different, non-parametric multiple comparisons (Siegel & Castellan 1988), all $P < 0.025$). For *C. glomerata* on *P. rapae* there was a significant effect as well of encounters on the residence time ((0, 1, 2 encounters), $P << 10^{-3}$, Kruskal-Wallis test; all pairs of groups are different, multiple comparisons, all $P < 0.01$). In both *Cotesia* species encounters with the solitarily feeding *P. rapae* larvae increased patch residence time.

DISCUSSION AND CONCLUSIONS

Initial search

When an inexperienced *C. rubecula* or *C.glomerata* female takes off for the first time, her informational state is incomplete. She seems incapable of long-distance discrimination between patches containing preferred and less preferred hosts (Geervliet *et al.* 1994). The present study aimed to address how parasitoids make patch leaving decisions on different types of patches and how experience modifies decision making.

C. rubecula

C. rubecula had the lowest leaving tendency on leaves containing the preferred host *P. rapae*. In the set-up with *P. brassicae* only, the leaving tendency was highest, both on empty and infested leaves. Thus, *C. rubecula* tends to spend a short time in unfavourable parts of its environment and will forage extensively in the good parts. In all three set-ups previous experiences, (i.e. the number of infested leaves visited and the total number of hosts encountered) did not affect the leaving tendency in the current patch.

C. glomerata

C. glomerata females had a lower leaving tendency on leaves containing the preferred host than on leaves infested with *P. rapae*. Patch leaving decisions in *C. glomerata* changed with experience. When a naive *C. glomerata* parasitoid foraged in an environment with *P. brassicae*, it had a lower leaving tendency on leaves containing feeding damage than on clean leaves. This tendency decreased after the parasitoid's first few ovipositions. During subsequent visits to infested leaves the leaving tendency increased. In the field, larval density on patches varies considerably: *P. brassicae* clusters can consist of anything between seven and 150 larvae. In such a variable environment it may be adaptive to use information on the quality of previously visited patches to adapt foraging decisions during subsequent patch visits. The increase in leaving tendency with the number of infested leaves visited in the *P. brassicae* set-up was strongest early in the experiments. This is in line with the predictions of the marginal value theorem. When more good patches are visited with relatively short travel times, the estimated value of the environment as a whole increases and consequently the leaving tendency should increase. *C. glomerata* switched to a simple rule in environments containing *P. rapae*: information on previous patch visits did not affect the leaving tendency in *P. rapae* environments.

Interspecific differences

The two parasitoid species showed interspecific variation in the way they made patch leaving decisions. *C. rubecula* had a higher leaving tendency than *C. glomerata* in all environments. The high leaving tendencies of *C. rubecula* fit well into a foraging strategy focusing on a solitary host. The generalist *C. glomerata* was more plastic in its decisions than the specialist *C. rubecula*.

Results compared to the models of Waage and Driessen *et al.*

In the patch exploitation mechanisms proposed by Waage (1979) and Driessen *et al.* (1995) the concentration of kairomone on a patch determines the initial responsiveness of the parasitoid. In environments where (i) patches contain reliable and detectable information on host availability or

(ii) contain a uniform number of hosts, a count-down mechanism (Driessen *et al.* 1995) would perform best (factor(i) being the key factor). When initial patch density assessment is inaccurate, it would be adaptive for the parasitoids to use an incremental mechanism, i.e. to prolong the time in the patch after ovipositions, as in Waage's (1979) model.

Previous experiments with *C. glomerata*, using individual females on single leaves and methods similar to Driessen *et al.* (1995), showed that the parasitoids did not have different leaving tendencies on leaves containing feeding damage from one or eight *P. brassicae* larvae (P=0.77, N_{d1}=15, N_{d8}=15, logrank test, Vos, unpublished data). This suggests that an incremental mechanism should be used. Indeed, ovipositions did prolong the time *C. glomerata* spent on a patch with *P. brassicae.* Waage's (1979) patch time model did not address the effects of factors as experience in previously visited patches or olfactory cues from the environment on patch time in the current patch. For *C. glomerata* these factors proved to be important. First of all patch leaving decisions changed as a function of experience acquired during successive patch visits. Secondly, patch leaving decisions were environment-dependent.

Neither of the two *Cotesia* species used a count-down rule in the environment with the uniform distribution of *P. rapae*. Several factors may prevent the evolution of a count-down rule.

(1) Kairomone concentration or feeding damage may be an unreliable source of information on host presence. Young *P. rapae* larvae for example face a high risk of mortality due to predation (Jones *et al.* 1987). A count-down rule would perform badly in a patch that was recently depleted by a predator.

(2) Detectability may be problematic. Driessen *et al.*'s patches were small (∅3,4 cm). A Brussels sprouts leaf is large (∅ up to 40 cm). The parasitoids may not be able to detect the concentration of leaf damage and kairomone on the entire leaf, when searching at a specific site. The results indeed show that although both *Cotesia* species stay longer on infested than on uninfested leaves, they do not significantly increase their residence time with larval density.

(3) The distribution of hosts across patches in the *P. rapae* environment (low density and variance) is not strictly uniform. Patches mostly contained one, two or three hosts. This may be too variable for the count-down rule to perform well.

Interestingly, in Driessen *et al.*'s (1995) study, *V. canescens* seems to have a higher efficiency on patches with four hosts than on patches with one host. This is not the case for either *Cotesia* species on *P. rapae*. The time until first oviposition (TUFO) did not differ significantly on patches containing different host densities. Therefore, time until first oviposition is not a reliable source of information on host density. There was no significant difference in the efficiency (number of encounters / patch residence time) on different host densities. On patches containing two or more hosts, the TUFO and time between first and second oviposition did not differ significantly either. An increased leaving tendency following an oviposition (as in a count-down rule) would only diminish the probability of finding another host on that same leaf. When the estimation of the damage level at low densities of *P. rapae* is inaccurate, and the time when ovipositions occur reveals little information on density or depletion, neither Driessen *et al.*'s (1995), nor Waage's (1979) patch exploitation mechanisms should be used. It may be better to adjust the leaving tendency to a cue like the presence or absence of feeding damage, and reset the leaving tendency after each oviposition to the initial value as it was set upon entering the patch. This is what both *Cotesia* species seem to do: on *P. rapae* there is no effect of density on the leaving tendency and encounters reset the leaving tendency, thereby prolonging the residence time with another $1/h(t;z)$ seconds (i.e. the new expected GUT).

A lack of reliable information on host density in a patch is will constrain the use of inter-patch information as well. Even if the animal has information on the value of patches in its environment through oviposition experiences, it may be impossible to use that information, because the value of the current patch relative to that of the 'average patch' is unknown. This may be the reason that neither *C. glomerata*, nor *C. rubecula* showed use of information on previous patch visits in the environment with *P. rapae* (with our covariates).

Adjustable termination rates

Based on the proportional hazards analysis, we propose the following patch exploitation mechanism for the description of the behaviour of *C. rubecula*.

1. Set a 'basic leaving tendency' to the available olfactory information in the environment while still in flight.
2. Land on a plant that releases olfactory and/or visual information on feeding damage.
3. Have a relatively high leaving tendency if the leaf is clean.
4. Have a lower leaving tendency if feeding damage is present (this decrement may also depend on the environmental olfactory information).

5. Have a stronger decrease in leaving tendency on a leaf containing the type of damage caused by the preferred host species.

6. Reset the leaving tendency after each oviposition, resulting in an expected GUT similar to what it was upon entering the patch (note that this does increase the residence time).

Go through the same cycle after taking off from the leaf. The steps involved in the leaving tendency (**1**, **3**, **4**, **5** and **6**) can be represented mathematically by an equation similar to the proportional hazards model (1). Factors involved in a tendency to arrive (like step **2**) can be formulated by essentially the same type of equation (Ormel, Gort & van Alebeek 1995). In adjustable termination rate models the animal is considered as continually adjusting its probability per unit time to leave (termination rate), according to "good" and "bad" experiences. The model can be used in simulations aimed at comparing the performance of complex and simple decision rules in different environments, taking into account the constraints on the animal's informational state. Step **2** of the model is supported by the analysis of Wiskerke and Vet (1994): first landings occur mostly on infested plants, and by extensive work on olfactory responses in these parasitoids (Steinberg *et al.* 1992; Geervliet, Vet & Dicke 1994; Geervliet *et al.* 1996). The proportional hazards analysis provided the evidence for steps **1**, **3**, **4**, **5** and **6**, and these steps are based on those covariates that had a significant effect on the leaving tendency.

C. glomerata will use a patch-exploitation mechanism rather similar to the one used by *C. rubecula* in environments containing only *P. rapae.* However, for *C. glomerata* it would be adaptive to learn to discriminate between the olfactory information released from *P. brassicae*- and *P. rapae*-infested plants in habitats containing both host species, and, at step **2**, land on leaves with the preferred host. Recently it was shown that *C. glomerata*'s response to *P. brassicae*-infested leaves does increase with oviposition experience in *P. brassicae* (Geervliet *et al.* 1996). As this parasitoid learns to prefer to land on *P. brassicae* patches, it may start to specialize on this host and treat environments containing both hosts like an environment containing solely *P. brassicae.* In such an environment *C. glomerata* differs from *C. rubecula* in a number of ways: (i) the leaving tendency decreases with ovipositions, in step **6**; (ii) the parasitoids use the more complex mechanism in which the use of information on previously visited patches is incorporated as well. For *C. glomerata* we propose steps **7**, **8** and **9**: Adjust the leaving tendency according to (i) the cumulative number of ovipositions experienced, (ii) the number of infested patches visited and (iii) time. The exact balance of these factors will depend on the amount of heterogeneity in the environment and may change as the parasitoid moves into richer or poorer parts of its environment.

Arrival and leaving tendencies

The analysis presented here focused on patch leaving decisions. Although a proportional hazards analysis of *arrival* tendencies is beyond the scope of this paper, it is clear that the efficiency of a patch leaving mechanism depends heavily on the tendency to arrive in certain patch types. Patch exploitation strategies can be thought of as balanced sets of effects of experiences on the tendencies to arrive in and leave certain microhabitats.

Termination rates of foragers are local in time and space. They depend on the animal's environment and may change as it gains experience and moves into other parts of its habitat. This is a source of behavioural variation that should not be ignored when considering the adaptive significance of animal decisions.

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3

Geographic variation in host acceptance in the parasitoid *Cotesia glomerata*: genotype versus experience

Summary

Host acceptance of two *Pieris* species was compared between two strains of the parasitoid *Cotesia glomerata*: one strain from the USA, where *C. glomerata* was introduced from Europe 117 years ago, and one native European strain. In the USA, larvae of *Pieris rapae* are attacked, while in Europe both *P. rapae* and *Pieris brassicae* serve as hosts. *P. brassicae* is the preferred host species, but since it is absent in the USA, it has as not been available to American *C. glomerata* for about 350 generations. We observed clear geographic variation in host acceptance between American and European parasitoid strains: American *C. glomerata* rejected *P. brassicae* significantly more often than European parasitoids did.

In addition we tested how experience modifies host acceptance in European *C. glomerata*, that have to deal with a relatively complex environment. Early experience through development in and emergence from a host clearly changed host acceptance: European *C. glomerata* showed a significantly higher acceptance of *P. rapae* when they were reared on *P. rapae* than when they developed in *P. brassicae*. Host acceptance increased after experience with the less preferred host, while acceptance of the preferred host was 'hardwired': It was high regardless of previous experience. Such strong inflexible responses to important stimuli and plastic responses to less important stimuli can be observed in many parasitoid-host systems. However, our results show that 350 generations of selection seem sufficient to override such hardwiring of responses.

A series of oviposition experiences with *P. brassicae* versus *P. rapae* larvae did not affect the acceptance of a subsequently offered *P. rapae* larva, nor did it affect the clutch size in this host.

Our results are discussed in the context of geographical variation in selection pressures, and compared with studies on information use in other parasitoid-host systems

INTRODUCTION

Classical biological control programmes can provide unique opportunities to test ecological and evolutionary hypotheses (Greathead 1986; Le Masurier & Waage 1993). Hundreds of generations after their release interesting comparisons can be made between natural enemies from the new and the original environment. Such comparisons between populations after prolonged exposure to different selection regimes can provide information on the magnitude of evolutionary change in traits (e.g. behaviour) at such a time scale, and on the mechanistic aspects of such change. One example of such a biological control project is the introduction of the parasitoid *Cotesia glomerata* in 1884 (Clausen 1956) from Britain to the USA to control the lepidopterous pest *Pieris rapae* that was accidentally imported from Europe and spread throughout Canada and the USA from the 1860s onwards (Chittenden 1916; Clausen 1956). Since its release *C. glomerata* has established itself within a few decades throughout most of North America.

In Europe, *C. glomerata* attacks the gregariously feeding larvae of the large white butterfly, *Pieris brassicae*, the solitary larvae of the small white, *Pieris rapae*, and to a lesser extent *Pieris napi*, in which field survival is low (Geervliet *et al.* 2000). In North America *P. brassicae* is absent and *P. rapae* the main host. *P. napi* can be attacked in the USA (R.G. Van Driesche pers. comm.). Both *P. brassicae* and *P. rapae* are suitable hosts for *C. glomerata* development (Brodeur, Geervliet & Vet 1998), but *P. brassicae* is the preferred host (E.A. van der Grift, M.P. Huijser & L.E.M. Vet, unpublished), and tends to sustain the development of larger clutches and larger wasps in a single larva (Harvey 2000). In Europe *C. glomerata* may experience seasons or years in which clusters of *P. brassicae* are extremely rare, while they can be abundant in others (Pak *et al.* 1989). This means that *C. glomerata* may have a choice between *P. brassicae* and *P. rapae* in some years or seasons, but cannot count on this choice to be available (Vos Chapter 5). It is an interesting question which mechanisms *C. glomerata* will use in order to determine whether it will actually accept *P. rapae* larvae, that it is more likely to encounter regularly, or that it will reject these as a host, to spare its eggs for a possible 'jackpot' cluster of *P. brassicae* larvae. It may not be adaptive to use a fixed decision rule like 'only accept *P. brassicae*'. Instead, female parasitoids may use various cues for the presence or absence of *P. brassicae* in the current environment: (i) They may have developed in *P. brassicae* or *P. rapae*, and have experienced characteristics of the host odour on their cocoon upon emergence (see Hérard *et al.* 1988); (ii) they may use an oviposition experience with *P. brassicae* as a cue to start rejecting *P. rapae*; (iii) they may use visual cues to discriminate between plants damaged by *P. brassicae* (large feeding holes) and *P. rapae* (small feeding holes) (J.Verdegaal, F. Wäckers & L.E.M.Vet, unpublished); and (iv) they may even learn to use subtle differences in plant volatile blends from *P. brassicae*- versus *P. rapae*-infested plants (Geervliet *et al.* 1998), and subsequently only accept larvae on plants with *P. brassicae*-damage. A combination of such cues could be used as well.

The spatial foraging behaviour of European *C. glomerata* seems more adapted to gregariously living *P. brassicae* larvae than to the solitarily feeding larvae of *P. rapae* (Wiskerke & Vet 1994; Vos, Hemerik & Vet 1998). They have a high tendency to repeatedly return to infested leaves (J.M.S. Burger & M. Vos unpublished; Vos Chapter 4 & 5), which can be adaptive when a leaf contains a large cluster of *P. brassicae*, but not when it only contains an already parasitised single *P. rapae* larva.

The percentage parasitism by *C. glomerata* in the field is usually higher for *P. brassicae* than for *P. rapae*, in Europe (Moss 1933; Richards 1940; Sengonca & Peters 1991; Geervliet *et al.* 2000). Geervliet *et al.* (2000) have hypothesised that host selection in *C. glomerata* is more focused on *P. brassicae* in Europe, to avoid intrinsic competition with *Cotesia rubecula*, a superior competitor in *P. rapae* (Laing & Corrigan 1987). This competitor is absent in most of the USA. Natural selection can be expected to have resulted in adaptation of the introduced *C. glomerata* population to foraging for the solitary host *P. rapae* in North America (Le Masurier & Waage 1993). North American parasitoids may have lost some characteristics of their behaviour that are especially tuned to foraging for highly clustered *P. brassicae* larvae (Vos Chapters 4& 5).

Le Masurier and Waage (1993) have shown that more than 100 years after their introduction, *C. glomerata* from the USA have a higher attack rate on *P. rapae* than British *C. glomerata* (in the laboratory). Their experiment consisted of confining the hosts with a parasitoid for 2 hours in a cage, after which larvae were dissected to determine levels of parasitism. The results from this 'black box' experiment were in agreement with the prediction that natural selection has changed the behaviour of *C. glomerata* in its new environment, where it attacks *P. rapae* in the absence of *P. brassicae*. However, these results did not provide any clue as to which aspects of parasitoid behaviour might be different between American and British strains of *C. glomerata*. Moreover, the American parasitoids used in the experiments had been reared on *P. rapae*, while British parasitoids were cultured on *P. brassicae*. The different environments experienced by immature parasitoids during development, and the different stimuli available to newly emerged parasitoids in early adulthood may have affected the outcome of the experiments (Le Masurier & Waage 1993).

One important aspect of parasitoid behaviour, that may affect attack rates, is host acceptance. Differences in host acceptance between the different strains of *C. glomerata* could explain the higher rate of attack as observed by Le Masurier & Waage. Therefore we decided to compare host acceptance between American and European *C. glomerata* parasitoids. We ask whether geographic variation in host acceptance exists between these populations, and whether the host species in which parasitoids develop has a phenotypic effect on host acceptance in the adult parasitoids. In addition we ask which mechanisms are used by European *C. glomerata* to make decisions on host acceptance in the more complex European environment. Our specific questions are: **1.** Do American and European strains of the parasitoid *C. glomerata* differ in their host acceptance of *Pieris rapae* and *P. brassicae*? **2.** Do European *C. glomerata* parasitoids show phenotypic differences in host acceptance after development in different host species (for one generation)? **3.** Do European *C. glomerata* use oviposition experiences in *P. brassicae* versus *P. rapae* as a cue to change subsequent host acceptance of *P. rapae*? **4.** Do geographic origin and developmental/early adult experience affect *C. glomerata*'s clutch size in *P. rapae*? **5.** Can we understand the results in the light of the different ecological environments in Europe and North America? **6.** Can we understand the mechanisms of host acceptance in the *Cotesia-Pieris* system in relation to mechanisms in other parasitoid-host systems?

MATERIALS & METHODS

The food plants were three-month-old Brussels sprouts plants (*Brassica oleracea* L. var. gemmifera cv. Icarus), grown in a greenhouse (20-25 °C, 50-70% RH , L16:D8). The host species were the small white, *P. rapae* and the large white *P. brassicae*, which originated from field collected individuals from the vicinity of Wageningen, The Netherlands, and were reared in a climate chamber (22-24 °C, 40-70% RH, L16:D8). The preferred first instar larvae of both host species were used in the experiments. The European parasitoid culture was established from *P. brassicae* larvae that had been placed in, and were recaptured from, Brussels sprouts fields near Wageningen, the Netherlands, during the summer of 1998. This collection yielded about 100 cocoon clusters (2000 parasitoids). This European strain of *C. glomerata* was continually reared on first instar larvae of *P. brassicae*, in a greenhouse compartment (21-25 °C, 50-70% RH, L16:D8). Parasitoid cocoons were stored at

12-13 °C; emerged parasitoids were kept in (40*30*30 cm) cages (23 °C, 50-70% RH, L16:D8). Ample water and honey was present. Each generation of parasitoids from the above strain was also allowed to oviposit in the alternative host, *P. rapae*. Thus we had also *C. glomerata* at our disposal that were reared on *P. rapae* for one generation, under the same conditions as described above.

The American strain of *C. glomerata* was established from 32 cocoon clusters, about 600 individuals, collected from 5th instar *P. rapae* from a white cabbage *Brassica oleracea* L. field in Geneva, New York, USA, and kindly sent to us by Mark Schmaedick and Tony Shelton in august 1997. The American *C. glomerata* parasitoids were continuously reared on Dutch *P. rapae* under the same conditions as the European strain. Both the European and the American parasitoid strain had been reared in the laboratory for several generations before being used in the experiments, thus probably purging maternal effects that might be due to the different original environments.

Experiment 1

The experiments were carried out in the laboratory at 23-24 °C, 40-50% RH, and 6000 Lux. For the experiments 3-5 day old mated female parasitoids were collected from the culture cages and individually held in a vial with wet cotton wool and a honey droplet. These parasitoids did not have prior experience with hosts or plant materials. They only had experience with the cocoons they emerged from. Just prior to an experiment, leaf areas (0.5-0.7 cm^2) containing a single host, either *P. rapae* or *P. brassicae*, and its feeding damage were cut out of infested Brussels sprouts leaves. Such a leaf disc was placed in the vial, where the parasitoid was allowed to walk onto it and search for the host. For each replicate a new parasitoid, vial and leaf disc were used. A parasitoid's first contact with the host occurred either through antennation, or a short external stab of the ovipositor, or by touching the host with the mouth parts. It was recorded whether first contact was followed by an insertion of the ovipositor into the host. Hereafter we will refer to this phase in behaviour as "antennal" acceptance. Walking away after first contact was recorded as antennal rejection. The duration of ovipositor insertions was measured to determine whether this could be used as a criterion for ovipositorial acceptance or rejection: After an ovipositor insertion each larva was dissected in water under a microscope, with a light source underneath the dissection slide, in order to count the number of parasitoid eggs present inside. When no eggs were observed, this was scored as ovipositorial rejection. When one or more eggs were found this was recorded as ovipositorial acceptance, which is host acceptance. Treatments: Six different treatments were used: European *C. glomerata* reared on *P. brassicae* or reared on *P. rapae* and American *C. glomerata* reared on *P. rapae* were tested on either *P. rapae* or *P. brassicae.* Thus it was possible to separate phenotypic effects (by development in different host species or early adult experience with cocoons), from genotypic effects (European versus American strains) on host acceptance. Each of the six treatments was replicated 36 times. All these 216 parasitoids made a first contact with a host larva.

Experiment 2

In experiment 2a we repeated treatments 1, 2 and 3 of experiment 1. In experiment 2b we measured the effect of a series of oviposition experiences with *P. rapae* versus *P. brassicae* on subsequent acceptance of *P. rapae* as a host. The experimental procedure was similar to that of experiment 1. Each parasitoid was allowed to walk onto a leaf disc that contained a single *P. rapae* or *P. brassicae* larva, and have an oviposition experience. This treatment was repeated two more times within about 30 minutes, each time with a new leaf disc and larva, so that each parasitoid had three oviposition experiences with larvae of a single host species. Subsequently, acceptance of *P. rapae* as a host was tested as in experiment 1. All parasitoids in this latter experiment had been reared on *P. rapae.* Experiment 2 differed from experiment 1 in that we used slightly larger infested leaf areas (about 1 cm^2); we observed antennal acceptance/rejection, but measured only part of the ovipositor insertion times. We dissected larvae as in experiment 1. For each treatment 30 replicates were performed.

Statistical analysis

Chi-square tests for 2 x 2 tables with Yates correction for continuity were used for host acceptance data. As some groups were used in a number of comparisons (n), differences were considered significant at P-values below 0.05/(n), the so-called Bonferroni correction. Clutch sizes were compared with a Multifactor Analysis of Variance. The three qualitative factors were: origin (US or Europe), experimental host (*P. rapae* or *P. brassicae*), and developmental host (*P. rapae* or *P. brassicae*). Clutch sizes following different oviposition experiences were compared using a Mann-Whitney U-test.

RESULTS

Experiment 1

Genotype versus early experience with the natal host

Table 1 shows the results for the parasitoids that were tested on *P. rapae*. Most of the European and American *C. glomerata* parasitoids that were reared on *P. rapae* accepted this host, at the level of antennal as well as ovipositorial decisions. There was no difference in host acceptance between the European and American strains, when they had been reared on the same host, *P. rapae* (P=0.54). European *C. glomerata* that were reared on a different host, *P. brassicae*, rejected *P. rapae* significantly more often than parasitoids of the same strain that had been reared on *P. rapae* for one generation (P=0.0039). European *C. glomerata* reared on *P. brassicae* also rejected *P. rapae* significantly more often than American *C. glomerata* reared on *P. rapae* (P<0.001, note: this is the same situation as in the experiment by Le Masurier & Waage (1993)).

Table 1 Host acceptance in a parasitoid strain from Europe (EUR) and one from the USA, tested on *P. rapae*, when reared on *P. brassicae* or *P. rapae*.

Strain origin, rearing host	Antennal rejection	Antennal acceptance	Ovipositorial rejection	Ovipositorial acceptance	**Total rejection**	**Total acceptance**	
EUR, *P. brass.*	10	26	11	15	**21**	**15**	a
EUR, *P. rapae*	2	34	6	28	**8**	**28**	b
USA, *P. rapae*	0	36	5	31	**5**	**31**	b

Different letters (a, b) indicate significant differences in (total) host acceptance.

Table 2 shows the results for the parasitoids that were tested on *P. brassicae*. Most of the European *C. glomerata* parasitoids, regardless of the host they were reared on, accepted *P. brassicae* at the level of antennal as well as ovipositional decisions. American *C. glomerata* that were reared on *P. rapae* significantly more often rejected *P. brassicae* than European *C. glomerata* that were reared on *P. rapae*, indicating geographic variation in the acceptance of *P. brassicae* between the two parasitoid populations (P<<0.001).

Table 2 Host acceptance in a parasitoid strain from Europe (EUR) and one from the USA, tested on *P. brassicae*, when reared on *P. brassicae* or *P. rapae*.

Strain origin, rearing host	Antennal rejection	Antennal acceptance	Ovipositorial rejection	Ovipositorial acceptance	**Total rejection**	**Total acceptance**	
EUR, *P. brass.*	0	36	3	33	**3**	**33**	a
EUR, *P. rapae*	0	36	1	35	**1**	**35**	a
USA, *P. rapae*	12	24	7	17	**19**	**17**	b

Different letters (a, b) indicate significant differences in (total) host acceptance.

Figure 1 shows the clutch sizes laid by American and European parasitoids, when tested on *P. brassicae* or *P. rapae*, after development in one of these hosts. None of the three tested factors had a significant effect on clutch size, (Mulifactor ANOVA, P_{origin}=0.14, $P_{experimental\ host}$=0.47, $P_{developmental\ host}$=0.93). Ovipositorial rejections could occur in two distinct intervals: after short times of 1-5 seconds 91% of the insertions were rejections, and after long times of 21-120 seconds 71% of the insertions were rejections. Almost all insertion times within the range of 6-20 seconds were ovipositions (99%).

Experiment 2

Genotype versus early experience with the natal host

The part of experiment 2 that repeated the three treatments of experiment 1 where acceptance was tested on the host *P. rapae*, yielded essentially the same results: *C. glomerata* rejected *P. rapae* more often after development in *P. brassicae* (χ^2, P=0.0068, while there was no difference between American and European parasitoids when both developed in *P. rapae* (χ^2, P=0.70), (Table 3).

Oviposition experience as a cue?

Our results showed that 27 out of 30 *C. glomerata* parasitoids antennally accepted *P. rapae* after three ovipositions in *P. rapae* (and development in *P. rapae*). Surprisingly, antennal acceptance of *P. rapae* still amounted 25 out of 30 times, after three ovipositions in *P. brassicae*. Thus a series of oviposition experiences in the preferred versus less preferred host did not significantly affect subsequent acceptance of *P. rapae* in a no-choice situation (χ^2, P=0.70, with Yates

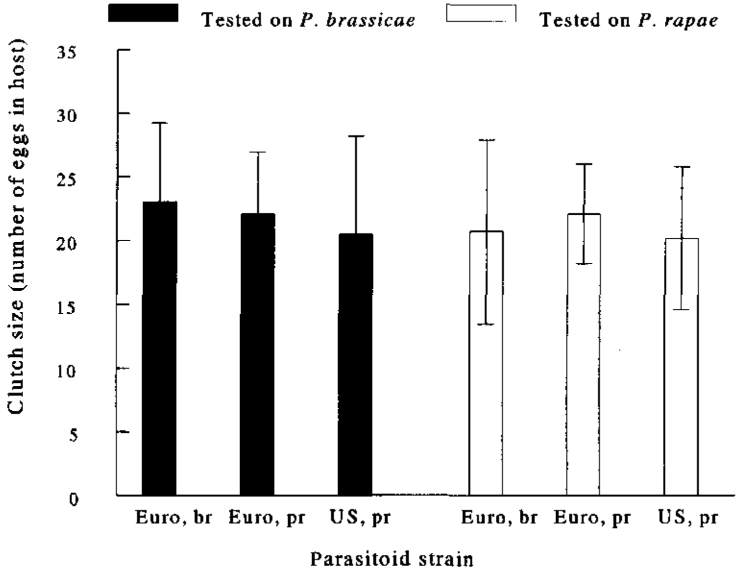

Figure 1 Clutch sizes in the hosts *P. brassicae* and *P. rapae* by parasitoids from Europe (Euro) and North America (US), that had developed in *P. brassicae* (br) or *P. rapae*, (pr). Error bars represent standard deviations.

correction for continuity). The average clutch size in *P. rapae* after a series of ovipositions in *P. brassicae* (16.6, $N_{dissected}$ = 17) did not differ significantly from the average clutch size after a series of ovipositions in *P. rapae* (16.3, $N_{dissected}$ = 12; MWU, P=0.93). The average size of the first clutch had been 24.8 ($N_{dissected}$ = 17) after development in *P. brassicae*, and 24.3 ($N_{dissected}$ = 12) after development in *P. rapae*. Apparently clutch size decreased from about 24.5 to about 16.5 after a series of three ovipositions.

Table 3 Host acceptance in a parasitoid strain from Europe (EUR) and one from the USA, tested on *P. rapae*, when reared on *P. brassicae* or *P. rapae*.

Strain origin, rearing host	Antennal rejection	Antennal acceptance	
EUR, *P. brassicae*	16	14	a
EUR, *P. rapae*	5	25	b
USA, *P. rapae*	3	27	b

Different letters (a, b) indicate significant differences in antennal host acceptance.

DISCUSSION AND CONCLUSIONS

Le Masurier and Waage (1993) found a higher attack rate on *P. rapae* in a US strain of the parasitoid *C. glomerata* when compared to a British strain, about 325 generations after its introduction from Britain to the USA. One of the main ecological factors that differ between the USA and Britain, is that the host *P. brassicae* is absent in the USA, while it is the preferred host of *C. glomerata* in Europe. Le Masurier and Waage (1993) have suggested that the higher attack rate on *P. rapae* in the US strain reflects adaptation to a situation where *P. rapae* is the main host, in the absence of *P. brassicae*. However, they could not rule out the possibility that differences in experience during parasitoid development or at emergence influenced the observed attack rates. The US *C. glomerata* developed in the same host they were tested on (*P. rapae*), while British *C. glomerata* developed in *P. brassicae*, but were tested on *P. rapae*. Chemicals emanating from parasitoid cocoons can provide emerging parasitoids with information that they use in host searching as adults (Hérard *et al.*1988; Turlings *et al.* 1993). So our question was, whether the observed differences in attack rates reflected true geographic variation among strains, or phenotypic variation due to differential experience.

Geographic variation versus early adult experience

When European and US parasitoids were reared and tested on *P. rapae*, they did not show any genotypic difference in acceptance of *P. rapae* as a host. Acceptance of *P. rapae* in European *C. glomerata* was already high when they were reared on this host, so US parasitoids could hardly 'improve' on this. However, when both strains were reared on *P. rapae*, but tested on *P. brassicae*, the US parasitoids significantly more often rejected *P. brassicae* than European parasitoids did. The US animals seem to have lost a great deal of their tendency to parasitise this host, that has not been available in the USA for several hundred generations. Parasitoids from the US strain often showed a different type of behaviour during the initial host acceptance phase: A first encounter by a US parasitoid often consisted of touching the host with its mouth parts while lowering its entire body over the host by flexing all legs. This behaviour was not observed in the European strain of *C. glomerata*, where first encounters occurred only by antennation or a short stab with the ovipositor. Interestingly, US *C. glomerata* that walked away and ignored *P. brassicae* after a first encounter, were highly motivated to continue searching on other parts of the leaf area with feeding damage and host by-products from this host. In fact they would not let themselves be easily removed from the leaflet. Apparently it is only the larva itself that is less attractive to the parasitoids. This also indicates that plant volatiles from the damaged leaf area may increase the tendency of a parasitoid to search, but do not play a decisive role in determining host acceptance in *C. glomerata.*

European *C. glomerata* rejected *P. rapae* significantly more often after development in *P. brassicae* than after having *P. rapae* as its natal host. This phenotypic effect of the developmental host may have played a role in the experiments of Le Masurier & Waage (1993), and may explain the observed difference in attack rates between British and US *C. glomerata*: British *C. glomerata* may have had a significantly lower attack rate on *P. rapae* due to their development in *P. brassicae.*

When we tested European *C. glomerata* on *P. brassicae*, most of the parasitoids readily accepted this host, irrespective of their natal host. This conforms with the notion of *P. brassicae* being the preferred host of *C. glomerata* in Europe.

Clutch size decisions

We did not find any difference in clutch sizes due to geographical origin or the host species our parasitoids were reared or tested on. Oviposition experiences did not significantly affect clutch size either. Some conflicting evidence exists on clutch size allocation in *C. glomerata.* Brodeur, Geervliet & Vet (1998) showed that European *C. glomerata* (reared on *P. brassicae*) produced larger clutch sizes on *P. brassicae* than on *P. rapae.* The parasitoids emerging from these larger clutches in *P. brassicae* did not differ in any life-history parameter from those emerging from the smaller clutches in *P. rapae*, which confirms *P. brassicae*'s role as a better host for *C. glomerata.* Harvey (2000) observed that European *C. glomerata* allocated larger clutches to *P. brassicae* than to *P. rapae*, and showed that wasps from *P. brassicae* tended to be larger. However, Brodeur & Vet (1995) did not find a difference in *C. glomerata* clutch size in *P. rapae* versus *P. brassicae.* Moreover, Le Masurier (1991) found the opposite, a higher clutch size of British *C. glomerata* (reared on *P. brassicae*) in *P. rapae* than in *P. brassicae.* Le Masurier did not observe a difference in clutch size between American and British *C. glomerata* in *P. rapae.* These results suggest that *C. glomerata* clutch size is highly dependent on the experimental set-up, procedure and state of the animals, and that clutch size is apparently not a major factor in adaptation of *C. glomerata* to the US environment.

Phenotypic variation after oviposition experience?

We expected that a series of ovipositions in the preferred host *P. brassicae* would lead to subsequent rejections of *P. rapae* as a host. However, three ovipositions in this host did not affect host acceptance relative to three ovipositions in *P. rapae*. Geervliet *et al.* (1998) showed that European *C. glomerata*, with *P. brassicae* as the natal host, did not have an innate preference for *P. brassicae*-infested plants, but did develop a landing preference for *P. brassicae*-infested Brussels sprouts leaves over *P. rapae*-infested Brussels sprouts leaves after two attack experiences with either *P. rapae* or *P. brassicae* larvae. It is possible that *P. brassicae* being the natal host was a necessary condition for this learning to prefer *P. brassicae*-infested leaves. Such learning of *P. brassicae*-specific plant odours might help *C. glomerata* to mainly deal with *P. brassicae*-patches after it has found this host for the first time.

Be that as it may, using a series of ovipositions as a cue for the presence of *P. brassicae* in the environment, is a bit of an 'a posteriori' way of dealing with information: If *C. glomerata* lands on a cluster of *P. brassicae*, it can probably deposit its entire egg complement in these preferred hosts. Learning to reject *P. rapae* would become rather irrelevant after such an event. So, oviposition experiences may not be a useful source of information for parasitoids that have to decide whether or not to accept the many *P. rapae* larvae they will most likely encounter before ever bumping into a cluster of their preferred host species. Maybe the only a priori information available to a parasitoid comes from the natal host: If odours on a parasitoid's cocoon indicate development in *P. brassicae*, that host may still exist as a population in the environment. We have seen that development in *P. brassicae* led to a significantly higher rejection of *P. rapae*, in two separate experiments. The preference of *C. glomerata* for *P. brassicae* (E.A. van der Grift, M.P. Huijser & L.E.M. Vet, unpublished) was observed using parasitoids that had developed in *P. brassicae*. We have no data for a choice situation after development in *P. rapae*, but our no-choice experiments show that *C. glomerata* mostly accepts *P. rapae* when this was the natal host. Based on the above results, we conclude that *C. glomerata* does not use ovipositions in *P. brassicae*, nor does it need to use these, to learn to reject *P. rapae* as a host. Moreover, *C. glomerata* does not need any experience with *P. brassicae* to learn to prefer this host: Even after development in *P. rapae*, and without any oviposition experience, 97 % of the parasitoids accepted *P. brassicae* for oviposition.

Geographical variation: North America versus Europe as an environment

From the viewpoint of *C. glomerata* the main ecological factors differentiating the US from Europe have been the absence of the clustered host *P. brassicae* and the parasitoid *C. rubecula* in the US. Both of these factors can be expected to lead to behavioural evolution of US *C. glomerata*. In the US there has been no selective advantage of focusing on cues specifically related to the presence of *P. brassicae* during host location, of retaining a high acceptance level for *P. brassicae*, or of maintaining behaviour that is efficient in the exploitation of patches with clustered hosts. *P. napi* may occur with several larvae on a leaf, but never in a cluster like *P. brassicae* (up to 150 larvae side by side). So, in North America *C. glomerata* will not experience the heterogeneity in larvae across plants as it may experience in Europe when *P. brassicae* is present.

Niche segregation between *C. glomerata* and *C. rubecula*

Geervliet *et al.* (2000) have suggested that *C. glomerata* and *C. rubecula* coexist by niche segregation in the Netherlands, with *C. glomerata* mainly using *P. brassicae* (if available), and *C. rubecula* mainly using *P. rapae*, as a result of *C. rubecula* outcompeting *C. glomerata* in *P. rapae* larvae. However, simulation results suggest that a majority of Netherlands *C. glomerata* will not encounter a cluster of *P. brassicae* within a lifetime (Vos Chapter 5). This indicates that there may be a strong selection pressure on *C. glomerata* to accept *P. rapae* as a host, especially in years that *P. brassicae* clusters are rare (most years, Pak *et al.* 1989, F. Karamaouna & M. Vos unpublished; L. Castricum, J.J.A. van Loon & M.Vos unpublished). The selection pressure imposed by intrinsic competition with *C. rubecula* in multi-parasitised hosts will depend on the parasitism levels *C. rubecula* can reach in *P. rapae*, and on the availability of *P. brassicae* in the environment. Preliminary field data suggest that parasitism levels by *C. rubecula* can be low (10%), at least in some years (L. Castricum, J.J.A van Loon & M. Vos, unpublished field data 1995). Further studies could show the probability that parasitoids of both species end up in the same larva in the field, at natural host densities. Differential use of *P. rapae* and *P. brassicae* in the field could also be due to a temporal domination of the *C. glomerata* population by parasitoids that have developed in, and emerged from a few clusters of *P. brassicae*. A single cluster of *P. brassicae* can potentially yield several thousand parasitoids, that, according to our results are highly likely to accept *P. brassicae* and reject *P. rapae* as a host. *C. glomerata* does not have this tendency after development in *P. rapae*. This suggests that host acceptance in *C.*

glomerata may be more tuned to the actual presence or absence of *P. brassicae* in the system than to avoiding intrinsic competition with *C. rubecula* in the Netherlands. However, one should be extremely careful when extrapolating laboratory host acceptance data to parasitism levels in the field (Bourchier & Smith 1996).

Fitness in *P. rapae* versus *P. brassicae*

Preliminary experiments did not show any difference in developmental time or survival in *P. rapae* and *P. brassicae* between the American and European strains. However, it is likely that *C. glomerata* has a considerably larger fecundity after development in *P. brassicae* than in *P. rapae*: Le Masurier and Waage (1993) found that British *C. glomerata* emerged with about 800 eggs after development in *P. brassicae*, which was considerably more than the 500 eggs in American *C. glomerata* that had *P. rapae* as their natal host. To rule out a genotypic effect, fecundity should also be measured in American *C. glomerata* reared on *P. brassicae*.

Acceptance in parasitoid-host interactions: population differences and the developmental host

Host acceptance has been studied extensively in parasitoid species that are used for biological control purposes (e.g. Bjorksten & Hoffmann 1995; Henter *et al.* 1996; Bjorksten & Hoffmann 1998; Rojas et al. 1999). Often these parasitoids are reared on a factitious host, that can be cultured more easily, but would not be found or parasitised in the field. Continuous rearing on a single host species may result in an micro-evolutionary 'experiment': The parasitoid strain may undergo selection pressures that tune it into using that host, possibly at a cost in traits for dealing with other (possibly the target (=natural)) host species, that could be encountered upon releases.

A strain of the parasitoid *Catolaccus grandis* showed a significant switch in host acceptance after only 10 generations of rearing on the factitious host *Callosobruchus maculatus*. This could not be reversed by rearing this parasitoid for a single generation on its natural host *Anthonomus grandis* (Rojas *et al.* 1999). The results of this study suggests that genetic changes in host acceptance can be very rapid, although it may also be a matter of many years. A population of the parasitoid *Encarsia formosa* that had been reared on the host *Trialeurodes vaporariorum* for many years accepted a lower percentage of *Bemisia tabaci* whitefly hosts than a population that had been reared for several years on *B. tabaci* (Henter *et al.* 1996). It is also possible that many of the foraging characteristics of the field population are retained, while the acceptance of the laboratory strain increases. A *Trichogramma minutum* strain that was collected from oblique-banded leaf roller eggs (*Choristoneura rosaceana*) had a much higher level of acceptance of this host than several *T. minutum* strains collected on other hosts. However, all parasitoid strains had a high level of acceptance of the rearing host *Ephestia kuehniella* (McGregor *et al.* 1998).

Bjorksten and Hoffmann (1998) found that parasitoid experience due to the rearing host or ovipositions altered the acceptance of low-ranked hosts, but not of highly preferred hosts in four strains of *Trichogramma brassicae*. A similar effect was observed in the parasitoid *Diachasmimorpha tryoni*: experience did affect host responses on less-preferred hosts, but not on preferred hosts (Duan & Messing 1999). This effect on the acceptance of only low-ranked hosts was similar in our *Cotesia-Pieris* system: experience due to rearing host did affect acceptance of the less preferred host *P. rapae*, but not of the preferred host *P. bassicae*. Apparently, acceptance of a high quality host is to some extent 'hardwired' in these systems while acceptance of a less preferred host is flexible, and can serve as a 'backup' under conditions where the best host is not available. However, our American parasitoids do not readily accept *P. brassicae* as a host. This trait may have been lost during the 350 generations *C. glomerata* did not have access to *P. brassicae* in North America. Behavioural differentiation between geographically separate populations often seems to occur by the loss of (parts of) behaviour patterns (Foster 1999). Crosses between populations of different geographic origins could illuminate the genetic contribution to variation in traits like host acceptance (Hopper *et al.* 1993). Such studies could lead to fundamental insights in local adaptation and lead to strategic knowledge that could be implemented to improve biological control practices

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4

Travelling behaviour in the parasitoid *Cotesia glomerata*: a comparison between American and European populations

Summary

Travelling behaviour was studied in American and European populations of the parasitoid *Cotesia glomerata*, in multi-patch environments with one of its hosts *Pieris rapae*. Also, patch leaving decisions were investigated in the presence or absence of an alternative high quality patch, with a cluster of *Pieris brassicae* larvae. This high quality host is present in Europe but not in North America.

European and American *C. glomerata* differ in the way they fly and orientate in space. European *C. glomerata* flew more often and hovered above more plants than their American conspecifics. European *C. glomerata* visited and searched many patches shortly, whereas American *C. glomerata* searched only a few patches thoroughly. Behaviour was more explorative in European *C. glomerata* and more exploitative in the American parasitoids.

C. glomerata travel times were longer between plants than within plants in European parasitoids, but not in the American strains. European *C. glomerata* frequently hovered across several plants before choosing to land, while flight in American parasitoids was often straight to a neighbouring infested plant. Travel times were short relative to patch residence times, in parasitoids from both geographical areas.

The presence of a high quality alternative patch had neither a measurable effect on patch leaving decisions, nor on other aspects of foraging behaviour. This suggests that foraging decisions on a patch are primarily based on local information.

Both American and European *C. glomerata* frequently revisited host-infested leaves. A substantial proportion of ovipositions was due to such revisits. This indicates that patch

exploitation consists of multistage decision making, where initial decisions are adjusted after parasitoids have dealt with (and learned on) several other patches in the local environment. Revisits may partly compensate for an initial lack of global information on the parasitoid's environment.

We discuss how the observed variation in foraging behaviour is related to different spatial distributions of *Pieris* hosts in Europe and North America.

INTRODUCTION

The exploitation of resources across patches is one of the central subjects of foraging theory (Stephens & Krebs 1986). Foraging animals cannot be assumed to have complete information on the distribution of resources, encounter rates with patches, rates of gain in different patch types, travel times, and many other aspects of their environment (Stephens & Krebs 1986). The fact that foragers do face incomplete information problems (sensu Stephens & Krebs 1986), has been dealt with by many authors, both theoretically and experimentally, f.e. (McNamara & Houston 1980; Iwasa *et al.* 1981; Lima 1983; Green 1984; Stephens & Krebs 1986; Mitchell 1989; Stephens 1989; Vet *et al.* 1998, Vos *et al.* 1998). Several studies have clarified how intra-patch experiences affect the decision to leave a patch in insect parasitoids (e.g. van Alphen & Galis 1983; Haccou *et al.* 1991; Hemerik *et al.* 1993; van Roermund *et al.* 1994; Driessen *et al.* 1995; Driessen & Bernstein 1999). Only a few authors have analysed parasitoid decisions in a multi-patch environment (Waage 1979; Wiskerke & Vet 1994; Vos *et al.* 1998), which is the natural context for foraging decisions. Observing parasitoid behaviour in multi-patch environments naturally provides information on travel times. Parasitoids may choose to travel within or between herbivore-infested plants, or hover across many plants and leaves to sample the environment for olfactory and /or visual information on the presence or distribution of hosts. Travel times are of utmost importance in determining the adaptive value of patch leaving decisions (e.g. Driessen & Bernstein 1999). Accurate estimates of parasitoid travel times are almost lacking in the literature (but see e.g. Völkl 1994; Völkl & Kraus 1996).

Patch exploitation consists of the whole cycle from entering one patch to entering another one. Thus it includes patch leaving, travel time and arrival decisions. Movement patterns across patches determine which information is experienced, while the available information may affect patch exploitation decisions. Parasitoid travel may be restricted to local flights between nearby patches, or involve hovering to sample a more extended area. The adaptive value of sample flights depends on the spatial distribution of host species. Distribution patterns of hosts can vary for at least two reasons: First of all, different host species may show pronounced differences in aggregation across patches. Secondly, the distribution of a single host species may differ markedly across geographical areas. Both factors play a role in the *Cotesia-Pieris* system: In Europe solitarily feeding *P. rapae* larvae follow a Poisson distribution across cruciferous plants (see Vos Chapter 5), while the preferred but rare gregarious host *P. brassicae* follows a heterogeneous distribution (highly clustered, with 7-150 larvae side by side on a leaf). In North America *P. rapae* has a Poisson distribution early and late in the season, and a negative binomial distribution during summer (but not nearly as clustered as the host *P. brassicae*, which is absent in North America, see (http://eap.mcgill.ca/CPCP_1.htm)).

The present paper has two aims. (i) We investigate travelling behaviour in parasitoid strains from two geographical areas with highly divergent spatial distributions of herbivorous hosts. Our analysis includes travel times within and between plants, and parasitoid arrival tendencies on infested plants and leaves (as opposed to empty plants and leaves). These data will be used in a companion paper where we model the effects of different travel strategies on life time reproductive success. (ii) To understand the observed travel patterns we study whether the parasitoids use olfactory information from an alternative, nearby patch of much higher quality, to make patch leaving decisions on the current patch. This should provide information on whether decisions are based on local information, (the current patch), or on simultaneous information from several patches in the local environment.

The system

In Europe, the parasitoid *Cotesia glomerata* attacks the clustered larvae of the large white butterfly, *Pieris brassicae*, and the solitary larvae of the small white, *Pieris rapae*. Of both host species, larval instars 1-3 (L_{1-3}) are highly suitable for *C. glomerata* development (Brodeur, *et al.* 1998). *P. brassicae* represents a richer resource than *P. rapae*, as one single *P. brassicae* larva can sustain the development of more female *C. glomerata* parasitoids, while other fitness parameters are equal (Brodeur *et al.* 1998). The foraging behaviour of European *C. glomerata* seems more adapted to the gregariously living larvae of *P. brassicae* than to the solitarily feeding larvae of *P. rapae* (Wiskerke & Vet 1994; Vos *et al.* 1998).

In North America *P. rapae* is the main host of *C. glomerata*. There *P. rapae* was first noticed in 1860, in Quebec (Scudder 1887). By 1886 it had spread as far south as the Gulf of Mexico, as far north as Hudson's Bay, and west to the Rocky Mountains (Scudder 1887; Harcourt 1963). It now occurs throughout most of North America (Harcourt 1963). In response to the ravages that *P. rapae* caused on cabbages, the parasitoid *C. glomerata* was intentionally introduced from Europe (well, from the UK), in 1884, near Washington DC (Clausen 1956). From there it quickly spread almost from coast to coast, now to be found in all sections of North America inhabited by its host (Clausen 1956).

Host densities are very different in Europe and North America: In Europe densities of *P. rapae* typically average between 0 and 1.6 eggs per plant (Pak *et al.* 1989). In the Netherlands we did not find more than 5 eggs or (L_{1-3}) larvae per infested plant, mostly 0, 1, or 2. The plants we sampled in *Brassica oleracea*-fields in the Netherlands had on average 40 leaves. Infested leaves contained mostly 1, less often 2, and rarely 3 (L_{1-3}) *P. rapae* larvae (L. Castricum, J.J.A. van Loon & M. Vos ; F. Karamaouna & M. Vos, unpublished field data). *P. brassicae* eggs or larvae typically occur in a few clusters (7-150) in a field, with an average of less than 0.15 per plant (Pak *et al.* 1989), or about 1 cluster per 200-300 plants (estimate based on Pak *et al.* 1989; field data L. Castricum, J.J.A. van Loon & M. Vos unpublished). In North America densities typically range from 0 to 30 *P. rapae* eggs per plant (Ontario, Harcourt 1961), and from 0 to 30 larvae per plant (New York State, van Nouhuys & Via 1999). Plants will on average contain 3-15 (L_{1-3}) larvae (Harcourt 1961). We have not found any information in the literature on the density of *P. rapae* at the level of leaves. However, Saskya van Nouhuys from Cornell University has sampled crucifers for *P. rapae* from 1992-1996, in New York State, where one of our American *C. glomerata* strains originates. "Most eggs are laid on big horizontal leaves in the sun, so if the butterfly density was high there could be 5 eggs on each of several leaves. During the peak of the season all plants in cultivated fields would be infested (and defoliated) if they had not been sprayed. Early and late in the season about 1 in 40 plants would be infested." (S. van Nouhuys, personal communication).

In Massachusetts, where our other American strain originates, the environment may be somewhat intermediate between Europe and New York State / Ontario. Average densities vary between 0.01 and 3 larvae per plant (Van Driesche 1988; R. Van Driesche pers. comm.). However, densities can be highly variable (which is more typical for the American situation) and the data in Van

Driesche (1988) may not be particularly representative for all other sites or years in Massachusetts (R. Van Driesche, pers. comm.). Another similarity between Europe and Massachusetts is the presence of *C. rubecula*. It has been introduced to Massachusetts by Van Driesche in 1988, in the area where our other *C. glomerata* strain originates (J. Benson, pers. comm.).

Le Masurier and Waage (1993) have shown that more than 100 years after its introduction, an equivalent of more than three hundred generations, *C. glomerata* from the USA have a higher attack rate on *P. rapae* than British *C. glomerata* (in the laboratory). Their experiment consisted of confining the hosts with a parasitoid for 2 hours in a cage, after which larvae were dissected to determine levels of parasitism. The results from this "black box" experiment conformed to the prediction that natural selection has changed the behaviour of *C. glomerata* in its new environment, where it attacks *P. rapae* in the absence of *P. brassicae*. However, it did not provide us with clues as to which aspects of parasitoid behaviour might be different between American and British strains of *C. glomerata*. Moreover, the American parasitoids used in the experiments had been reared on *P. rapae*, while British parasitoids were cultured on *P. brassicae*. The different environments experienced by immature parasitoids during development, and the different stimuli available to newly emerged parasitoids in early adulthood may have affected the outcome of the experiments (Le Masurier & Waage 1993). Parasitoid cocoons may emit different odours after parasitoid development in different host species. Parasitoids may use the infochemicals from their cocoons as a cue for host and patch quality later in life, and adjust patch exploitation decisions accordingly.

Questions

Using the *Cotesia-Pieris* system, we specifically address the following questions: 1. Do American and European *C. glomerata* show different patterns of movement across patches? 2. Do travel times differ between parasitoid strains, and between host-infested leaves within and between plants? 3. Do the parasitoids use (volatile) information from nearby patches while making foraging decisions on the current patch? 4. Does development in different host species affect foraging decisions in the adult parasitoids?

MATERIALS & METHODS

The European *C. glomerata* cultures were established from *P. brassicae* larvae that had been placed in, and were recaptured from, Brussels sprouts fields near Wageningen, the Netherlands, during the summer of 1997. This collection yielded about 100 cocoon clusters, about 2000 parasitoids. This European strain of *C. glomerata* was continually reared on first instar larvae of *P. brassicae*, in a greenhouse compartment (21-25 °C, 50-70% RH, L16:D8). Parasitoid cocoons were stored at 12-13 °C; emerged parasitoids were kept in (40x30x30 cm) cages (22.5-23.5 °C, 50-70% RH, L16:D8).Ample water and honey was present. Each generation of parasitoids from the above strain was also allowed to oviposit in the alternative host, *P. rapae*. Thus we had also *C. glomerata* at our disposal that were reared on this host for one generation, under the same conditions as described above.

The European strain of *C. rubecula* was established from *P. rapae* larvae that had been placed in, and were recaptured from, Brussels sprouts fields near Wageningen, the Netherlands, during the summer of 1997. This collection yielded about 100 solitary cocoons, and the same number of parasitoids.

One American strain of *C. glomerata* was established from 32 cocoon clusters, about 600 individuals, collected from 5th instar *P. rapae* from a white cabbage field in Geneva, New York, USA, and kindly sent to us by Mark Schmaedick and Tony Shelton in august 1997. Geneva is about 400 km from the original release site of *C. glomerata* in the United States.

The other American strain of *C. glomerata* was established from three cocoon clusters, 55 individuals, collected from cabbage fields near Amherst field station in Massachusetts, and kindly sent to us by Roy van Driesche in august 1997. Both American *C. glomerata* strains were continuously reared on *P. rapae* under the same conditions as the European strain.

The food plants were three-month-old Brussels sprouts plants (*Brassica oleracea* L. var. gemmifera cv. Icarus). Brussels sprouts plants were grown in a greenhouse (20-25 °C, 50-70% RH, L16:D8). The host species were the small white, *P. rapae* and the large white *P. brassicae*. They were reared at 22-24 °C, 60-70% RH and a L16:D8 photoregime. The preferred first instar larvae of both host species were used in the experiments.

Preparations for experiment 1

At the start of each experimental day, 3-10 day old mated female parasitoids were collected from the culture cages and individually held in a vial with wet cotton wool and a honey droplet. The parasitoids (in vials) were transferred to the experimental set-up and tested after at least half an hour of acclimatization. These parasitoids did not have prior adult experience with hosts or plant materials. They only had experience with the cocoons they emerged from.

Set-up experiment 1

The foraging behaviour of *C. glomerata* parasitoids was observed in a "semi-field set-up" with *P. rapae*-infested cabbage plants in a greenhouse compartment.. The set-up consisted of six Brussels sprout plants placed on a table in two parallel rows. Three of these plants were clean, while the other three were infested. The distance between plants was about 45 cm. Two fans placed at the end of the table provided an air stream of 0.2-0.3 $m \cdot s^{-1}$ at the parasitoid release site. This release site, situated at the downwind end of the table, consisted of a Brussels sprouts leaf disc with feeding damage of one early first instar *P. rapae* larva (the larva was removed). The distance between the release site and the first two experimental plants was about 30 cm. In this set-up parasitoid flight responses were above 90 %. *Brassica oleracea* leaves had a diameter of about 12 cm. Each infested plant had two infested leaves, each containing two larvae (so always four hosts per plant, two hosts per leaf). Five strains of *Cotesia* parasitoids were tested in this environment: (i) European *C. glomerata* (strain from Wageningen, the Netherlands) cultured on *P. brassicae*; (ii) European *C. glomerata* (strain from Wageningen, the Netherlands) cultured on *P. rapae*; (iii) American *C. glomerata* (strain from Geneva, New York State) cultured on *P. rapae*; (iv) American *C. glomerata* (strain from Amherst, Massachusetts) cultured on *P.rapae*; (v) European *C. rubecula* (strain Wageningen, the Netherlands) cultured on *P. rapae*. All strains were collected in the field, the summer before the start of the experiments.

The foraging behaviour of individual parasitoids was observed and recorded continuously. Each observation started at the moment the parasitoid left the release site and flew to a plant. Five minutes after the beginning of each experiment wind speed was reduced to 0.2 $m \cdot s^{-1}$ at the two experimental plants closest to the release site. At this wind speed the parasitoids could hover freely across the six plants in the experimental environment. Observations were terminated after 45 minutes or when the parasitoid left the foraging arena, landed elsewhere and remained there for more than two minutes, or when it remained motionless for more than two minutes within the set-up. For each parasitoid strain 21 to 24 females were tested.

Preparations for experiment 2

Female parasitoids were treated exactly as in experiment 1, but were in addition given experience with a host. Just prior to an experiment, leaf areas (about 10 cm^2) containing both feeding damage and a single *P. rapae* larvae were cut out of infested Brussels sprouts leaves. Such a leaf disc was placed in a petri dish, where the parasitoid was allowed to walk onto it and parasitize the host. After 15 to 30 minutes this procedure was repeated with another leaf disc and larva. Parasitoids not accepting the larvae for oviposition were excluded from the experiments. Geervliet *et al.* (1998) found that after two ovipositions in *P. rapae* or *P. brassicae C. glomerata* is able to discriminate between leaves infested with *P. rapae* and *P. brassicae* from a distance. Thus, giving parasitoids this experience can help them to learn to discriminate between backgrounds containing only *P. rapae*, or both *P. rapae* and *P. brassicae*.

Set-up experiment 2

The foraging behaviour of *C. rubecula* and *C. glomerata* parasitoids was observed in a "semi-field set-up" consisting of five Brussels sprouts plants in a greenhouse compartment. Four of these plants were arranged in a square on a table. These provided an infochemical background that either simulated an American or a European environment: In the European background three plants were infested with one *P. rapae* larva, while the fourth plant was infested with a cluster of 13 *P. brassicae* larvae. In the American background all four plants had one leaf infested with four *P. rapae* larvae. Two fans placed at the end of the table provided an air stream of 0.2 $m \cdot s^{-1}$ at the experimental leaf on the fifth plant, which was placed at the downwind end of the table. On this plant parasitoid behaviour was observed, on a leaf that contained 0, 1, or 8 *P. rapae* larvae. In the European background the plant with *P. brassicae* was always one of the two plants closest to the experimental fifth plant. The distance between the experimental fifth plant and the first two background plants was about 60 cm.

All larvae were carefully placed on the plants with a fine brush 24-30 hours in advance of the experiments. For the European environment we chose *P. rapae* density 1 as this is the most common density in the field. For the American environment we chose *P. rapae* density 4 per plant as: (i) It is within the range of averages per plant for New York state, the origin of the American parasitoid strain; (ii) it is within the range of peak densities for Europe; (iii) it contrasts very well with the experimental densities 1 and 8: should the parasitoids be able to detect host density from a distance, these densities should allow for clear differences in behaviour. The high experimental density of 8 larvae was chosen because this is likely to be the maximum density on a leaf that can be encountered in nature. If parasitoids show similar behaviour on densities 1 and 8, they probably do the same along the entire range of natural host densities on leaves.

The foraging behaviour of individual parasitoids was observed and continuously recorded with a handheld microcomputer, using Observer software (Noldus information technology 1993). Each observation started when the parasitoid walked out of the vial onto the centre of the experimental leaf on the fifth plant. An observation was terminated: 1) When the parasitoid left the experimental leaf, landed somewhere else and remained there fore more than one minute, or 2) when the wasp sat motionless for more then 5 minutes. We consider the start of such a period as a decision by the parasitoid to stop foraging. From experience we know that a wasp is unlikely to resume foraging in the next hours once it has assumed such a motionless position. A total of 200 parasitoids was observed: 66 to 67 females for each strain divided over 3 densities and 2 backgrounds.

Notation

Below we will refer to European *C. glomerata* cultured on *P. brassicae* as strain Eurobras, to European *C. glomerata* cultured on *P. rapae* as strain Eurorap, to North American *C. glomerata* from NewYork state as strain US_{NY}, and to American *C. glomerata* from Massachusetts as strain US_{Mass}.

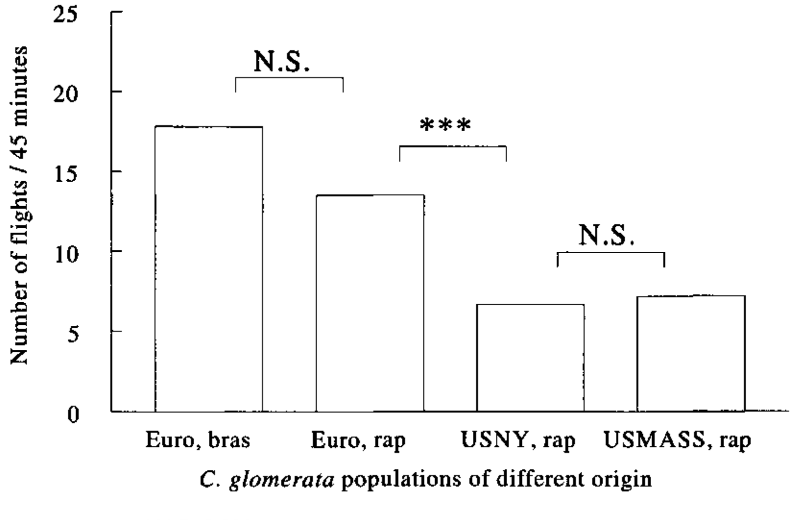
Statistical analysis

Most of the data were analyzed with generalized linear models (GLMs) using procedure GENMOD in SAS 6.11 (SAS Institute Inc. 1996). We corrected for slight differences in protocol duration with an offset (logtime) statement. Multiple comparisons were made using contrast statements. In the analysis of experiment 1 we performed planned contrasts between strains Eurorap and Eurobras, Eurorap and US_{NY}, and US_{NY} and US_{MASS}. For paired observations we used the Wilcoxon signed-ranks test (WSR, e.g. for observations on travel times within and between plants in the same parasitoid, with significance at P=0.05). In a few cases a Mann-Whitney U test (MWU) was used. For the analysis of experiment 2 we performed planned contrasts between strains Eurorap and Eurobras, and Eurorap and US_{NY}. Differences were considered significant at P=0.05/n, in the case of (n) multiple comparisons (contrasts). This is a (conservative) Bonferroni correction for multiple comparisons.

RESULTS

Experiment 1 movement patterns

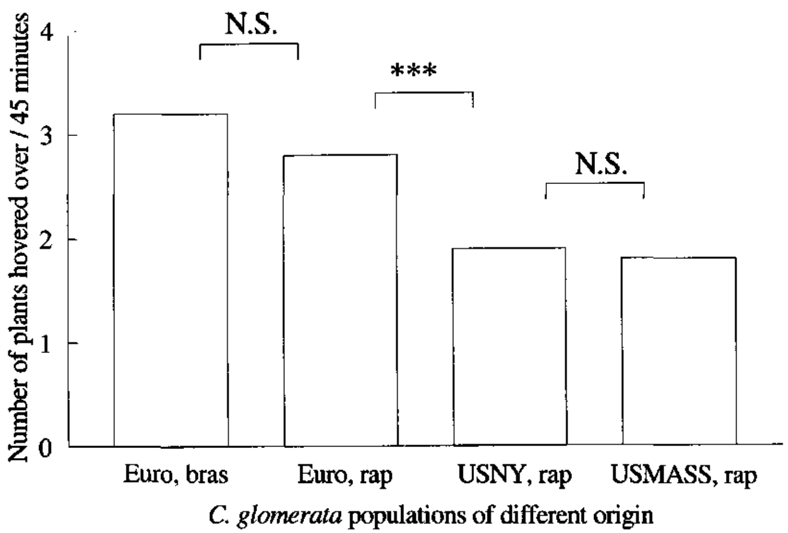
American and European *C. glomerata* parasitoids showed clear differences in the tendency to fly: Strains US_{NY} and US_{MASS} flew on average 6.7 and 7.2 times during 45 minutes of observation, while strains Eurobras and Eurorap flew 17.8 and 13.5 times in the same period, see Figure 1. The difference between strains Eurorap and US_{NY} was significant. There was no difference in the number of flights between strains from the same geographical area (GLM: $P_{Eurorap-}$ US_{NY} = 0.0008; $P_{USNY-USMASS}$ = 0.69; $P_{Eurobras-Eurorap}$ =0.09).



*** P<0.001

Figure 1 The number of flights in a multi-patch environment by different *C. glomerata* strains from Europe and North America after development in *P. brassicae* or *P. rapae*.

During an experiment, strains US$_{NY}$ and US$_{MASS}$ hovered on average in front of 1.9 and 1.8 different plants, while strains Eurobras and Eurorap hovered in front of 3.2 and 2.8 different plants, see Figure 2. Again, the difference between strains Eurorap and US$_{NY}$ was significant; while there was no difference in hovering between strains from the same geographical area (GLM: P$_{Eurorap\text{-}}$ US$_{NY}$ = 0.0001; P US$_{NY}$ - US$_{MASS}$ = 0.88; P$_{Eurobras\text{-}Eurorap}$ =0.45).



*** P<0.001

Figure 2 The number of plants hovered over in a multi-patch environment by different *C. glomerata* strains from Europe and North America after development in *P. brassicae* or *P. rapae*.

During each inter-plant flight, strains US$_{NY}$ and US$_{MASS}$ hovered on average in front of 1.3 and 1.2 different plants, while strains Eurobras and Eurorap hovered in front of 2.2 and 2.0 different plants. The difference between strains Eurorap and US$_{NY}$ was marginally non-significant; while there was clearly no difference in hovering between strains from the same geographical area (GLM: P$_{Eurorap\text{-}}$ US$_{NY}$ = 0.018 (the critical P= 0.0167, using the conservative Bonferroni correction); PUS$_{NY\text{-}USMASS}$ = 0.80; P$_{Eurobras\text{-}Eurorap}$ =0.11).

The strains US_{NY} and US_{MASS} made on average 0.6 and 0.65 revisits to host-infested leaves, while strains Eurorap and Eurobras made on average 1.7 and 3.8 revisits. The difference between strains Eurorap and US_{NY} was just not significant, while the number of revisits was significantly higher in strain Eurobras than in Eurorap (MWU: $P_{\text{Eurorap-}}\ US_{NY} = 0.021$;

The above mentioned tendencies to fly across patches caused strains US_{NY} and US_{MASS} to make on average 3.0 and 2.8 visits to host-infested leaves, while strains Eurorap and Eurobras made on average 4.7 and 6.2 visits The difference between strains Eurorap and US_{NY} was significant, while there was no difference in the total number of patch visits between strains from the same geographical area (MWU: $P_{\text{Eurorap-}}\ US_{NY} = 0.0080$; $P\ US_{\text{NY-USMASS}} = 0.65$; $P_{\text{Eurobras-Eurorap}} = 0.021$).

With each flight between plants, the probability to arrive at an infested plant was 0.67 in strain US_{NY} and 0.68 in strain US_{MASS}. This arrival probability was 0.6 in strain Eurorap and 0.85 in strain Eurobras. With each flight to leaves on infested plants, the probability to arrive at infested leaves was 0.89 in strain US_{NY} and 0.29 in strain US_{MASS}. This arrival probability was 0.76 in strain Eurorap and 0.62 in strain Eurobras.

Experiment 1 travel times

Travel times between plants were longer than travel times within plants in the European strains of *C. glomerata* (WSR: $P_{\text{Eurobras-within-between}} = 0.033$, $P_{\text{Eurorap-within-between}} = 0.012$). Average travel times from leaf to leaf were 46 seconds within plants, and 125 seconds between plants, in strain Eurobras. Flights lasted on average 35 seconds within plants, and 77 seconds between plants in strain Eurorap, see Figure 3. There was no significant difference in travel times between versus within plants in the North American strains (WSR: $P\ US_{\text{NY-within-between}} = 0.72$, $P_{\text{USMASS-within-between}} = 0.45$). Average travel times were 21 seconds within plants, and 26 seconds between plants, in strain US_{NY}. Flights lasted on average 30 seconds within plants, and 39 seconds between plants in strain US_{MASS}, see Figure 3. Travel times between plants were significantly different between strains Eurorap and US_{NY} (MWU: $P_{\text{Eurorap-}}\ US_{NY} = 0.00068$), but not between strains from within Europe and North America (MWU: $P\ US_{\text{NY-USMASS}} = 0.85$; $P_{\text{Eurobras-Eurorap}} = 0.77$). Parasitoids from strain Eurorap travelled more times between plants than parasitoids from strain US_{NY}: 2.5 versus 1.6 times, (MWU: $P=0.0041$), and also had a higher proportion of travel between plants: 0.51 versus 0.25, (MWU: $P=0.0057$).

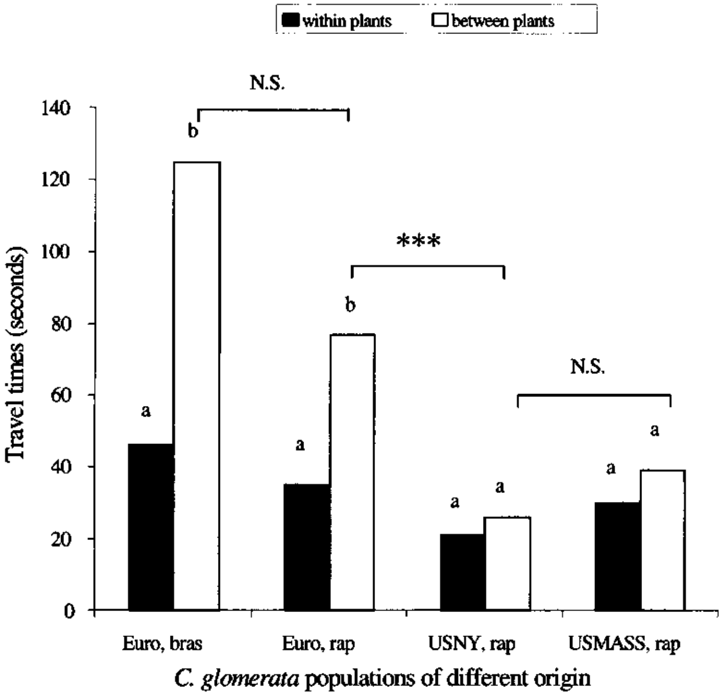


Figure 3 Travel times: the duration of flights from leaf to leaf, within and between plants by different *C. glomerata* strains from Europe and North America after development in *P. brassicae* or *P. rapae*.

Experiment 2 local information and patch exploitation.

We compared foraging decisions on *P. rapae*-infested leaves in the presence or absence of a nearby (60 cm) high quality alternative patch with a cluster of *P. brassicae* larvae. We tested strains US_{NY}, Eurorap and Eurobras, on experimental leaves containing 0, 1, or 8 *P. rapae* larvae. Patch residence times at host density 0 did not differ among strains (GLM: P=0.86), nor was there any effect of the alternative patch in the background. There was a significant effect of strain and density on residence times in host-infested patches (GLM: P_{strain} =0.0001, $P_{density}$ = 0.0004). Background information and interaction effects were not significant (GLM $P_{background}$ = 0.70, $P_{strain*density}$ = 0.99, $P_{strain*\ background}$ =0.13, $P_{density*background}$ = 0.80). Residence times did not differ between the two European strains (GLM: $P_{Eurobras-Eurorap}$ =0.46), but differed significantly between strains Eurorap and US_{NY} (GLM: $P_{Eurorap-}$ US_{NY} = 0.0004). Patch residence times increased from about 140 seconds on empty leaves to about 630 seconds on leaves with host density 8, in the European parasitoids. Patch residence times increased from about 170 seconds on empty patches to about 1500 seconds on patches with eight hosts, in the North American strain (Fig 4).

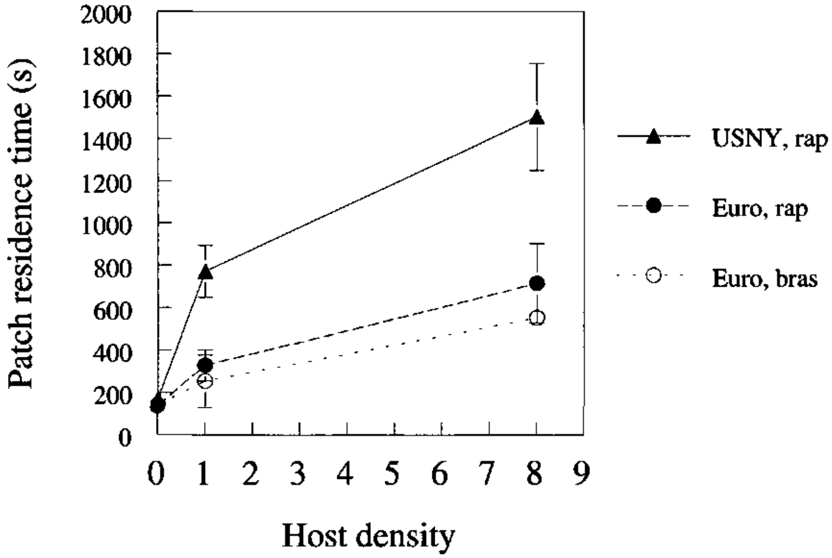


Figure 4 Residence times on leaves, at different densities of the host *P. rapae* by different *C. glomerata* strains from Europe and North America after development in *P. brassicae* or *P. rapae.*

There was a significant strain effect on the number of ovipositions per patch visit, both at host density 1 (GLM: P= 0.0034) and host density 8 (GLM: P=0.0016). In neither case was there an effect of background information (GLM: P= 0.48, P=0.36). Strain US_{NY} had a higher number of ovipositions per patch visit than strain Eurorap, both at density 1 and density 8 (GLM: P= 0.004, P= 0.014). The two European strains did not differ in the number of ovipositions per patch visit, neither on density 1, nor on density 8 (GLM: P=0.77, P=0,23).

DISCUSSION

Travel decisions are a key component of patch exploitation mechanisms. Optimal foraging models often implicitly assume that travel times are imposed by the environment (see e.g. Iwasa *et al.* 1981; Stephens & Krebs 1986; Driessen & Bernstein 1999). In such model approaches natural selection is assumed to optimize decisions on the search time in each patch as a function of the average travel time between patches. Our results show that travel time is not always an environment-imposed fact of life, but that it can rather be a decision variable itself. Parasitoids have a choice to travel within or between (herbivore-infested) plants. Furthermore, they have a choice in how much time to allocate to interplant flights, before choosing to land on another patch. We studied travel patterns in *C. glomerata* parasitoid strains from Europe and North America, in a multi-patch environment. The European strain Eurorap hovered in front of more plants, had more and longer inter-plant travel times, a higher proportion of inter-plant travel times, and visited more host-infested leaves than the North American *C. glomerata* strain US_{NY}, in the same environment. This suggests that parasitoids from different strains are likely to build an entirely different internal representation of an identical environment: The European parasitoids experienced many patches, searching each patch for a short time, while the American parasitoids searched only a few patches thoroughly. The US_{NY} parasitoids had more ovipositions per patch visit than the Eurorap parasitoids. American *C. glomerata* often flew straight to a neighbouring plant, while European *C. glomerata* frequently hovered in front of several plants before landing.

These differences in spatial foraging behaviour give the impression of a more explorative strategy in the European parasitoids, and a more exploitative strategy in the North American parasitoids. The adaptive value of patch exploitation mechanisms is intimately tied to the spatial distribution of resources (e.g. Iwasa *et al.* 1981; Driessen *et al.* 1995; Vos *et al.* 1998, Driessen & Bernstein 1999). Spatial distributions of *Pieris* hosts differ markedly in Europe and North America: In Europe *P. rapae* follows a Poisson distribution across plants, while the preferred (but rare) high quality host *P. brassicae* occurs in a few clusters in a field. In North America *P. rapae* follows a Poisson distribution early and late in the season, but a negative binomial distribution with higher densities per plant during midsummer (Harcourt 1961; S. van Nouhuys pers comm, see Vos Chapter 5).

We hypothesise that the extended inter-plant hovering in European *C. glomerata* is a means to facilitate location of *P. brassicae* in Europe, as volatile information might be easier to perceive or use when hovering in and out of an odour plume. As a first step, our second experiment intended to test whether the parasitoids use olfactory information from a nearby patch, while making decisions on the current patch. We showed that there was no measurable effect of a high quality *P. brassicae*-infested patch on the patch leaving tendency in *C. glomerata* parasitoids, even though it would be highly adaptive to quickly leave a poor patch for a high quality patch only 60 cm away. Preliminary experiments showed that the responsiveness to an infested leaf is highest from a distance of 0-30 cm in *C. glomerata*. This is also the distance at which parasitoids hover across leaves. These results suggest that extended hovering might be an essential feature for locating a nearby cluster of *P. brassicae*. Such inter-plant hovering was most pronounced in European *C. glomerata* that had developed in *P. brassicae*. This suggests that *C. glomerata* uses early experience with *P. brassicae* as a cue to the presence of this preferred host in the environment, and adjusts its searching behaviour accordingly (also see Vos Chapter 3). In North America explorative flights may not pay-off, as flight is likely to be costly, both in terms of energy and the risk of mortality (see Völkl & Kraus 1996; Weisser & Völkl 1997), while a benefit in the form of rare high quality host clusters is absent in this environment.

The above mentioned results indicate that foraging decisions are primarily based on local information, and that *C. glomerata* parasitoids do not simultaneously process olfactory information from several nearby patches while making decisions in the current patch. However, *C. glomerata* parasitoids frequently revisited patches after several visits to other patches. This can potentially facilitate information use on a larger spatial scale. Although it is not immediately clear whether revisits lead to a higher pay-off than visits to new patches, this result is important from a theoretical point of view. Initial patch leaving decisions as observed within a limited experimental timeframe, may not represent the final decision of a parasitoid for that patch. Patch exploitation can consist of multistage decision making, where initial decisions are adjusted after the parasitoids have dealt with (and learned on) several other patches in the local environment. The revisits in our experiments are not due to depletion within, or confinement to the multi-patch environment. If we did not stop the experiment after 45 minutes, the parasitoids would mostly intensely search the set-up for several hours before flying to the ceiling, still leaving a considerable proportion of hosts unparasitised.

Our results indicate that parasitoids may initially use highly local information, but make final exploitation decisions at the level of an area consisting of several patches. In a following paper we will explore the effects of local information processing, different travel patterns and multistage decision making on parasitoid life-time reproductive success in environments with different spatial distributions of hosts.

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5

Linking foraging behaviour to lifetime reproductive success for an insect parasitoid adaptation to host distributions

Summary

European and American populations of the parasitoid *Cotesia glomerata*, that forage for hosts with different spatial distributions, show pronounced differences in foraging behaviour across plants and leaves. This variation was observed about 350 generations after *C. glomerata*'s introduction from Europe to North America. We used simulation models to study how these behavioural differences affect lifetime reproductive success in environments with different host distributions. The larval host *Pieris rapae* follows a negative binomial distribution across plants, with 1-5 larvae per infested leaf during the summer in North America, and a Poisson distribution, with typically 1 larva per infested leaf early and late in the season. The host *P. rapae* has a Poisson distribution across plants in Europe. The preferred gregarious host *P. brassicae* is present in Europe, but not in North America. This host occurs in rare clusters of 7-150 larvae on a single leaf.

Our simulations showed that the foraging strategy of American *C. glomerata* resulted in a higher lifetime reproductive success on a Poisson *P. rapae* distribution than the strategy of European *C. glomerata*. Lifetime reproductive success did not differ between populations on a negative binomial *P. rapae* distribution. Our results suggest that *C. glomerata* has adapted to the North American environment through the loss of explorative traits that are necessary to locate rare clusters of *P. brassicae* in Europe. American parasitoids spend less time on exploration and more time on exploitation of patches.

Lifetime reproductive success of the European strategy was most sensitive to an increase in the giving up time (GUT) on infested leaves. American parasitoids differed most from their European conspecifics in exactly this behavioural parameter and showed a 121% higher GUT.

In our first simulations parasitoids could not discriminate from a distance between different host densities on infested plants and leaves. In following simulations we allowed the parasitoids to perceive information on plant and/or leaf damage levels in their local environment, and to use this information to preferentially land on high-density patches. Lifetime reproductive success did not significantly increase under such an increased perception and use of information.

Our simulations suggest that North American parasitoids are mostly time-limited early and late in the season and mostly egg-limited in the middle of the season. We discuss our results in the light of behavioural adaptation, under incomplete information, to different spatial distributions of resources.

INTRODUCTION

A central question in foraging theory is how strategies for the exploitation of patchily distributed resources are related to the reproductive success of foraging animals. Many parasitoid species exploit herbivorous insect larvae in plant canopies. These host larvae can occur in hierarchical patches, consisting of plants and leaves. Travel times from leaf to leaf can be smaller within plants than between plants. In many studies of foraging and patch exploitation, only the decision of when to leave a patch is taken into account (e.g. Charnov 1976; Iwasa *et al.* 1981; Haccou *et al.* 1991; Hemerik *et al.* 1993; Driessen *et al.*1995; Rodríguez-Gironés & Vásquez 1997; Vos *et al.* 1998; Driessen & Bernstein 1999). However, the adaptive value of patch leaving decisions may be closely linked to patch arrival (Vos *et al.* 1998) and travel time decisions. In an hierarchically structured environment parasitoids can choose to travel within or between plants, which implies a choice in the type and magnitude of travel times (Vos Chapter 4). In optimal foraging models a performance function is often used that maximises the long-term rate of offspring production (E), given a certain giving up-rule:

$$E = \frac{N}{(Ttravel + Tsearch)} \qquad \text{eqn 1}$$

where N is the average number of offspring per patch, T_{travel} is the average travel time between patches and T_{search} is the average time spent searching in each patch (Iwasa *et al.* 1981; also see Stephens & Krebs 1986; Driessen & Bernstein 1999). Natural selection is assumed to optimise decisions on T_{search} as a function of T_{travel} , where T_{travel} is supposed to be imposed by the environment (Iwasa *et al.* 1981). However, under a hierarchical patch structure the actual optimisation problem does not only involve decisions on T_{search}, depending on T_{travel} . Instead, the problem involves the simultaneous optimisation of decisions on both T_{search} and T_{travel} . These decisions should depend on the distributions of hosts across plants and leaves, which do impose minimal travel times within and between plants, but also on the costs (energy, time and wear) and possible benefits (information acquisition) of longer than minimal travel times.

Previous experiments have shown pronounced differences in decisions on T_{travel} and T_{search} between European and American populations of the parasitoid *Cotesia glomerata.* European parasitoids typically hover and hop across many plants and leaves and have short residence times, while the American parasitoids fly much less and search more persistently within infested plants (Vos Chapter 4). *C. glomerata* travel times are longer between plants than within plants in European parasitoids, but are not different in the American population. European parasitoids tend to hover across several plants before choosing to land, and thus have longer travel times between plants than American parasitoids.

The European wasps have a higher tendency to return to previously visited infested leaves (Vos Chapter 4). In many theoretical studies (e.g. Charnov 1976; Iwasa *et al.* 1981; Rodríguez-Gironés & Vásquez 1997) the assumption is made that revisits to patches do not occur and that foragers make one leaving decision, that is final, on each patch. However, parasitoids of our European population of *C. glomerata* revisit host-infested leaves up to four times, and those of our North American population up to two times, after visits to other patches. This indicates that patch-exploitation can be a process of multistage decision making, with early patch decisions being adjusted during later visits (Vos Chapter 4). The possibly adaptive value of revisits and decisions to travel within or between plants is intimately tied to the spatial distribution of hosts. Host distribution does impose a certain amount of travel time and will thus affect a parasitoid's time budget. This will in turn affect how natural selection acts on life history decisions like investments in eggs and survival, and affect the proportions of time limitation and egg limitation in a parasitoid population. It is important to know whether a parasitoid population is mostly time-limited: many theoretical studies assume time limitation, which implies that natural selection acts on traits affecting parasitism rates. The distribution of *Pieris* caterpillars can vary considerably with geographical area, season and the particular species involved and parasitoids have to deal with this variation.

General aims

Our general aim is to relate the variation in foraging behaviour between American and European parasitoids to variation in lifetime reproductive success. We investigate the performance of both foraging strategies on the different host distributions occurring in North America and Europe. Furthermore we check how lifetime reproductive success changes when we vary the amount of information a parasitoid can have on its environment.

The system

The parasitoid *C. glomerata* is indigenous to Europe and was introduced in North America from Europe in 1884, about 350 *C. glomerata* generations ago. In Europe, *C. glomerata* parasitises larvae of *Pieris brassicae* and *Pieris rapae*. Its repertoire of spatial foraging behaviour seems adapted to the gregarious larvae of *P. brassicae* and is much less efficient on the solitarily feeding *P. rapae* larvae (Wiskerke & Vet 1994). *P. brassicae* clusters are rare in most years (Pak *et al.* 1989). A cluster occurs on about one in every 200-300 *Brassica* plants (calculation based on Pak *et al.* 1989 and L. Castricum, J.J.A. van Loon & M. Vos, unpublished field data). This implies that a *P. brassicae* cluster could be present on about one in every 20-30 *Pieris*-infested plants (see below). *P. rapae* occurs at low densities in Europe, with averages around 0.1 *P. rapae* per plant (Pak *et al.* 1989; Karamaouna & Vos unpublished), and peaks in averages reaching 1.6 per plant (Pak *et al.* 1989).

C. glomerata attacks *P. rapae* in North America, since *P. brassicae* is absent there, *P. rapae* occurs at low densities early and late in the season in North America (S. van Nouhuys, pers. comm.). The distribution of *P. rapae* across plants agrees well with a Poisson distribution at densities below two per plant (Harcourt 1961). In the middle of the season North American *P. rapae* populations reach high densities, having a negative binomial distribution, with means of 3-16 (L_{1-3}) larvae per plant (Harcourt 1961). Densities on leaves range from one to five (S. van Nouhuys, pers. comm.), versus a typical density of one L_{1-3} larva per leaf when *P. rapae* population densities are low (F. Karamaouna & M. Vos unpublished). North American *C. glomerata* have been suggested to have evolved a higher attack rate than European *C. glomerata*, on *P. rapae* (LeMasurier & Waage 1993).

Specific aims and questions

Firstly, we use a simulation model to evaluate the lifetime reproductive success resulting from alternative foraging strategies in two geographically distinct parasitoid populations. The model is based on data from foraging experiments in multi-plant environments with European and North American *C. glomerata* parasitoids and literature/field data on host distributions in Europe and North America. Our model explicitly incorporates the hierarchical structure of patches and parasitoid exploitation patterns within such structure. We specifically ask: **1.** How is lifetime reproductive success in parasitoids from Europe and North America affected by the distribution of *P. rapae* hosts across plants and leaves? **2.** Is the foraging strategy of the American population more successful in the North American environment than the European strategy about 350 generations after *C. glomerata*'s introduction to North America? **3.** What is the proportion of time-limited animals in European and American parasitoid populations under Poisson and negative binomial host distributions?

Secondly, we use this model to study parasitoid lifetime reproductive success under different ecological scenarios. In these scenarios we ask questions on decisions in parasitoids as well as in hosts. We vary: (i) the amount of information available to the parasitoids, (ii) host decisions on how to distribute their offspring, and (iii) the eggload available to female parasitoids. We specifically ask: **4.** Would the ability to perceive and use information on host infestation levels on plants and/or leaves in the local area lead to an increase in lifetime reproductive success? This is particularly imporant for the American population that has to deal with a heterogeneous host distribution in the middle of the season **5.** Would such an ability have a higher pay-off if it spanned a wider local environment? **6.** Would the host's decision to always have single eggs on leaves reduce parasitisation rates by North American parasitoids? **7.** To which aspects of parasitoid behaviour is lifetime reproductive success most sensitive? **8.** How would variation in fecundity further differentiate the foraging success of North American *C. glomerata* on a Poisson and a negative binomial distribution of hosts?

MATERIALS & METHODS

We constructed a model for simulating the foraging behaviour of an individual *C. glomerata* female, during her entire lifetime. She forages in a field of 3025 *Brassica oleracea* plants (55 plants long and 55 plants wide) and makes patch arrival and leaving decisions both at the spatial scale of plants and leaves. In order to answer each of our questions we varied certain characteristics of the basic model: a) the foraging behaviour characteristic for each strain (American or European), b) host distribution, c) use of information on host densities, d) fecundity (egg load). The behaviour of each parasitoid is stochastic. We simulated 100 parasitoid lifetimes for each ecological scenario. Below we provide our methods in three sections, two for the description of the experimental and literature data we used for the model, and one describing the model itself.

Experimental data

We used the results of two experiments (see Vos Chapter 4 for details) to parameterise the foraging model. In the first experiment we observed individual *C. glomerata* females foraging on a single leaf on a *Brassica oleracea* plant with host densities of zero, one or eight *P. rapae* larvae (*N*=22 for each treatment). We used results of parasitoids from two different populations: one from the USA, (Geneva, New York state), and one from Europe (vicinity Wageningen, The Netherlands). Parasitoids of both strains had been reared on *P. rapae*, under identical climatic conditions. Both strains had been in the laboratory for several generations before being used in the experiments, thus purging maternal effects that might be due to the original environment. In the experimental background, four *Pieris*-infested plants provided alternative patches to go to, in case the parasitoid decided to leave the current patch. This experiment provided data on: 1) giving up times on empty leaves (GUT_{empty}), 2) giving up times on infested leaves ($GUT_{infested}$), 3) intervals between ovipositions (IBOs). These are either the time until the first oviposition on a patch, or the time between ovipositions.

In the second experiment we allowed individual *C. glomerata* females to forage in a multi-patch environment consisting of six *B. oleracea* plants for 45-60 minutes. Three of these plants were infested with four *P. rapae* larvae. The infested plants had two infested leaves, each containing two larvae. We used the same strains as in the first experiment (*N*=22 for each parasitoid strain). The multi-patch experiment provided data on 1) travel times between plants and within plants, 2) the probabilities to travel between versus within plants, 3) probabilities to fly to empty versus infested plants, 4) probabilities to fly to empty versus infested leaves, 5) the probabilities of revisiting infested leaves, 6) the same type of data as the single patch experiment (see above). We will call the Wageningen population 'European', and the Geneva population 'American', for convenience, and to emphasise that these populations have geographical origins that differ in ecological conditions.

Literature data

Cass and Harcourt provide extensive data on population densities and distributions of *P. rapae* in North America. Cass (1960) found averages of 1.9 and 4.3 larvae per cabbage plant, in two years, in untreated plots. Harcourt found on average 3-16 (L_{1-3}) *P. rapae* larvae per cabbage plant, over a five-year period, in insecticide-free plots, (Harcourt 1961, 1962). For the variance-mean relationship of a negative binomial distribution the expectation of the variance is: $s^2 = m + m^2/k$. Harcourt's estimate of k is 2.91 for the first three instars of *P. rapae*, which are the most suitable host stages for *C. glomerata*. Based on Harcourt's (1961) variance-means data (see his figures 1 and 2) we have chosen an average of m=5 and k=2.91 as the values we used in our simulations, to create a negative binomial distribution of larvae across plants. The variance-mean relationship of a Poisson distribution gives the expectation of the variance as $s^2 = m$. We estimated the mean density on a plant to be 0.1 for the European distribution, based on the data of Pak *et al.* (1989), and our own 1997 field data ($m=0.10$, $s^2=0.11$, F. Karamaouna & M. Vos unpublished). Harcourt (1961) showed that *P. rapae*'s distribution agrees well with a Poisson distribution at such low densities. We used a mean and variance of 0.1 L_{1-3} *P. rapae* per plant to simulate a European field distribution or an American distribution early or late in the season.

The Lifetime Foraging Model

We modeled a realistic spatial environment consisting of plants and leaves, and the behaviour of parasitoids within such structure, including revisits to patches and travelling within and between plants. This environment consisted of a field of 55 by 55 plants with a defined host distribution, either a Poisson distribution or a negative binomial distribution of *P. rapae* larvae across plants. Under the Poisson distribution plants contained zero, one, or two hosts. Individual leaves contained zero or one host. Under the negative binomial distribution plants contained 0-13 hosts per plant. Individual infested leaves contained 1-5 larvae (distr. $NB_{multiple}$). Especially to answer question 2), whether a (negative binomial) host distribution with only a single egg on each leaf would affect parasitoid lifetime reproductive success, we also simulated the same negative binomial distribution of hosts across plants, where only a single larva per infested leaf was present (distr. NB_{single}). We compared the European and American foraging strategies in environments where only *P. rapae* is present (as did le Masurier & Waage 1993). This facilitated a straightforward comparison of the efficiency of both strategies on *P. rapae*, but note that part of especially the European foraging strategy may be tuned to exploiting the potential presence of *P. brassicae* in the environment (see discussion). Our simulations start with releasing a parasitoid on the plant in the middle of the field. This parasitoid has either the behavioural strategy of the USA strain, or that of the European strain. The foraging parasitoid exploits the plants and leaves in the field subject to: (i) a probability of intra-plant travel when on an infested plant, (ii) a probability of intra-plant travel when on an empty plant, (iii) a probability to choose between neighbouring infested versus empty plants, either landing randomly with respect to host density on infested plants (iii, a), or with a probability proportional to host density (iii, b) The parasitoids can choose to land on one of the eight surrounding plants (in a 3x3 plant block), or one of the 24 surrounding plants (in a 5x5 plant block), thus allowing parasitoids to make choices at different spatial scales, (iv) a probability to choose between infested and empty leaves, either landing randomly with respect to host density on infested leaves (iv, a), or with a probability proportional to the density on infested leaves (iv, b).

Thus parasitoids can either have no information on host densities, just partial information (only at the plant or leaf level), or 'complete' information, (both at the plant and leaf level, also see discussion). Note that this information is not truly complete as it only concerns the local environment (8 or 24 surrounding plants). In the most simple 'default' situation the parasitoids have no information on surrounding plant and leaf damage levels. They only discriminate between 'infested' and 'clean', and make landing choices among the eight surrounding plants.

On empty leaves the parasitoid 'draws' a giving up time (GUT_{empty}), a travel time and travels. On infested leaves, the parasitoid draws a $GUT_{infested}$ and an interval between ovipositions (IBO). If the IBO is shorter than the $GUT_{infested}$, an oviposition occurs, with a clutch size of 20 eggs (Vos Chapter 3), according to the drawn IBO. Else the parasitoid leaves after the drawn $GUT_{infested}$. This drawing of GUTs and IBOs continues until a shorter $GUT_{infested}$ is drawn, or all hosts on the patch are parasitised, upon which the parasitoid leaves. Each parasitoid is allowed to forage an entire lifetime, drawn from an exponential distribution with an average of 86400 seconds, (=24 hours=three foraging days of eight hours, see Vos Chapter 1, our parasitoids live on average three days in a cage in the field (Geervliet 1997) and are most active between about 8 am and 4 pm, Vos personal observation). We simulated parasitoids with 500, 1000, 1400, 1500, 2000, 2500 or 3000 eggs. *C. glomerata* female fecundity varies between 500 and 2200 eggs (Moiseeva 1976; Shapiro 1976; LeMasurier & Waage 1993; Laing & Levin 1982; Tagawa 2000). Our 'default' parasitoid has an egg complement of 1400 eggs. We do not incorporate a trade-off between fecundity and longevity in our simulations, as the necessary experimental data are not available. However, we will show graphs on lifetime reproductive success for the full range of life spans and fecundities.

The above steps are summarised in a flow diagram (Figure 1), that shows the behavioural cycle of the parasitoid. Finally, we show all used parameter values in Table 1, and discuss these in the Appendix. Using these parameters, our simulations provided results on 'emerging' parameters like numbers of ovipositions and visits to infested plants and leaves that were satisfactorily similar to our experimental results (Table 2). Note that both the real behaviour in the experiment and the simulations are stochastic and could give different results if they were run again. The above check is not a validation but shows we modelled what we intended to model.

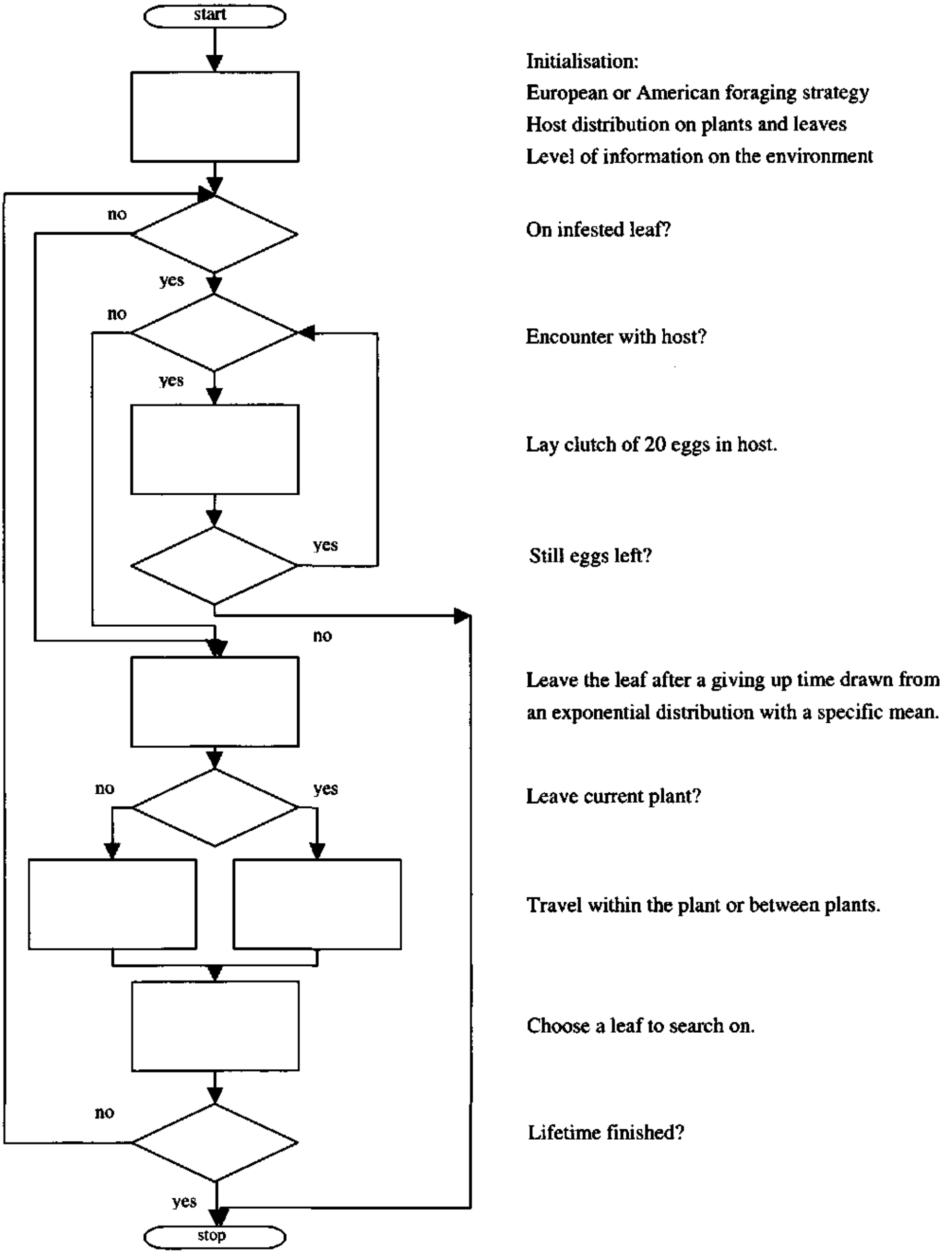

Figure 1 Flow diagram of the foraging behaviour of a *C. glomerata* parasitoid in a field with hierarchical patches (hosts are distributed across plants and leaves)

Table 1 Parameter values used in the simulations, based on experiments with American (Am) and European (Eur) *C. glomerata* parasitoids (Vos Chapter 4) and calculations in the appendix. All parameters involving time were fitted to an exponential distribution. Last column shows the percentage change from the European to the American value.

	Am, Eur		Change from Eur to Am value
Intrinsic intervals between ovipositions	671, 903,	(seconds, mean of exp. distr.)	-26 %
Intrinsic giving up times on infested leaves	855, 387,	(seconds, mean of exp. distr.)	+121 %
Intrinsic giving up times on empty leaves	185, 137,	(seconds, mean of exp. distr.)	+35 %
Travel times within plants	21, 35	(seconds, mean of exp. distr.)	-40 %
Travel times between plants	26, 77	(seconds, mean of exp. distr.)	-66 %
P(go to infested plant)	0.67, 0.60		+12 %
P(go to infested leaf)	0.89, 0.76		+17 %
P(stay on infested plant)	0.76, 0.65		+17 %
P(stay on empty plant)	0.47, 0.26		+81 %
P(1st revisit to infested leaf)	0.50, 0.99		-49 %
P(2nd revisit to infested leaf)	0.25, 0.50		-50 %
P(3rd revisit to infested leaf)	0, 0.25		
P(4th revisit to infested leaf)	0, 0.063		
Locally perceived environment	8, 24	(surrounding plants, for both strains)	
Information use on host density	none, only on plants, only on leaves, both on plants and leaves		
Fecundity, both strains	500, 1000, 1400, 1500, 2000, 2500, 3000 (eggs)		
Foraging lifetime	86400	(seconds, mean of exp. distr.)	

Table 2 Results of 45 minute stochastic simulations (N=100) of foraging behaviour in our experimental set-up, compared to actual experimental results (N=22). We show 'emerging' parameters (averages and standard deviations) resulting from the used parameter estimates.

	Number of ovipositions	Number of visits to infested plants	Number of visits to infested leaves
Data Am.	3.2 (1.2)	1.6 (0.71)	3.0 (1.4)
Simulation Am.	3.0 (1.5)	1.9 (1.0)	3.5 (1.5)
Data Eur.	2.0 (1.0)	2.5 (1.3)	4.7 (2.5)
Simulation Eur.	2.2 (1.5)	3.0 (1.3)	4.6 (1.7)

Statistical analysis

We used N=100 replicates for each ecological scenario. The results from different ecological scenarios or parasitoid populations were compared using a Kruskal Wallis test (KW, nonparametric analysis of variance). Subsequently nonparametric multiple comparisons were performed (Siegel & Castellan 1988). We chose to use the KW-test as our data on lifetime fitness could not be transformed to approach a normal distribution. We used the Mann-Whitney U test (MWU) for several comparisons of two samples. If samples were used in several (n) comparisons, we adjusted the P-level to 0.05/n (Bonferroni correction). For ease of reading we will use the term 'parasitoids' and 'strains' when presenting the outcome of our simulations. These terms refer to the particular foraging strategies we modelled for the North American and European *Cotesia glomerata* parasitoids. We will use the terms 'reproductive success' and 'fitness' meaning the number of eggs laid during the entire lifetime of parasitoids in our simulations.

Sensitivity analysis

We tested the sensitivity of lifetime reproductive success to an increase or decrease of 10 % in the value of each behavioural parameter. We did this for both the European and the American foraging strategy, in a Poisson environment. The default behavioural parameter values were as in Table 1, while fecundity was 1400 eggs. Animals used no information on host densities from a distance and chose to land among the eight surrounding plants. A single set of simulations consisted of 100 parasitoid lifetimes. Sets with (identical) default parameter values were replicated ten times for both the American and European foraging strategy, to check how much variation in lifetime reproductive success we can expect between sets due to stochasticity alone. The sensitivity was analysed for ten behavioural parameters. The sets for an increase or decrease of 10 % in a single parameter value were compared with the default set, using a MWU-test and a P-level of 0.025. Each default set had been designated to a particular behavioural parameter prior to the simulations. The sensitivity analysis entailed 60 sets of 100 simulations.

RESULTS

European and American fitness on different host distributions

Host distribution significantly affected lifetime reproductive success for both the European and American *Cotesia glomerata* foraging strategies (KW, $P=9.0 \cdot 10^{-6}$ and $P=4.2 \cdot 10^{-5}$).

European 'parasitoids' laid on average 876 eggs in the negative binomial environment with multiple larvae per leaf, 731 eggs in the negative binomial environment with single hosts on leaves, and 523 eggs in the Poisson environment, see Figure 2. Multiple comparisons showed significant fitness differences between the $NB_{multiple}$ and the Poisson environment, and between the NB_{single} and the Poisson environment. There was no significant difference in reproductive success between the $NB_{multiple}$ and NB_{single} environments.

American 'parasitoids' laid on average 950 eggs in the negative binomial environment with multiple larvae per leaf, 770 eggs in the negative binomial environment with single hosts on leaves, and 694 eggs in the Poisson environment, see Figure 3. Multiple comparisons revealed that lifetime reproductive success for the American strain was significantly different between the $NB_{multiple}$ and NB_{single} , and between the $NB_{multiple}$ and Poisson environments. There was no significant difference in reproductive success under the NB_{single} and Poisson host distributions.

The American strategy resulted in a higher fitness than the European strategy on the Poisson distribution (MWU, P=0.011). Reproductive success did not differ between parasitoid strains on the negative binomial distribution ($NB_{multiple}$), (MWU, P=0.14).

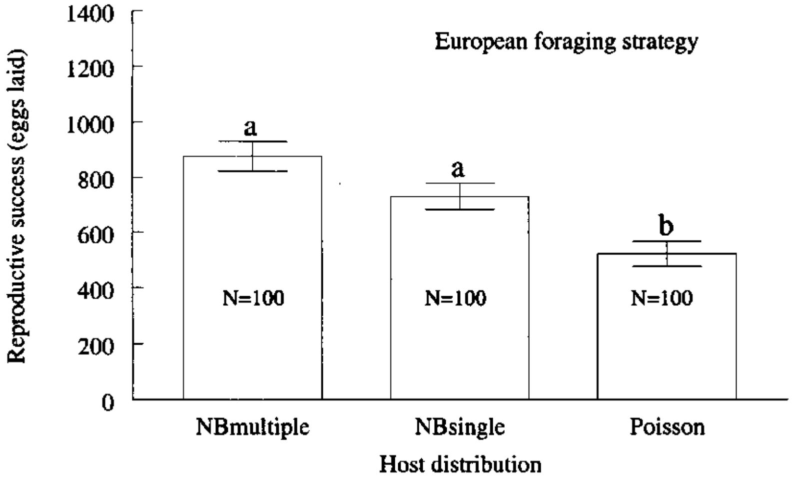

Figure 2 Parasitoid lifetime reproductive success (average ± standard error) of the European *C. glomerata* foraging strategy on different host distributions across plants: negative binomial (NBmultiple and NBsingle indicate the density of larvae on leaves) or Poisson. Different letters indicate significant differences.

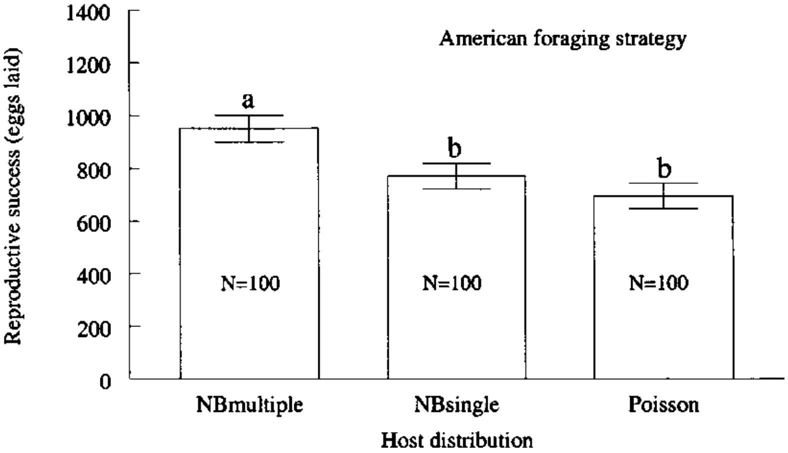

Figure 3 Parasitoid lifetime reproductive success (average ± standard error) of the American *C. glomerata* foraging strategy on different host distributions across plants: negative binomial (NBmultiple and NBsingle indicate the density of larvae on leaves) or Poisson. Different letters indicate significant differences.

Incomplete information

We considered several ecological scenarios where parasitoids either had (and used): no olfactory information on feeding damage levels in their local environment, only partial information, focusing on either plants or leaves, or complete olfactory information on the local environment, both at the level of plants and leaves. The 'informed' parasitoids used cues on host density to preferentially land on higher density patches. In our simulations, 'uninformed' parasitoids of both populations landed on plants with an average density of 5.3 hosts and on leaves with on average 2.9 hosts in the negative binomial environment ($NB_{multiple}$). Parasitoids visited plants with an average density of 7.0 hosts when informed on plant damage, and visited leaves with on average 3.3 hosts when informed on leaf damage. An improved informational state did not result in any significant difference in lifetime reproductive success, neither for the European, nor for the American strain, on any of the three host distributions (KW, all $P>0.05$).

In these simulations parasitoids perceived the eight surrounding plants as the local environment. We also allowed American parasitoids to perceive 24 instead of eight surrounding plants (a 5 by 5 local environment instead of 3 by 3), both under a Poisson and a negative binomial distribution. This did not lead to a significant change in lifetime reproductive success (MWU, $P=0.58$, $P=0.50$).

Lifetime reproductive success: Variability and sensitivity to behaviour

Lifetime reproductive success varied considerably among the ten default sets of 100 simulations of a parasitoid life time, due to the stochasticity of behavioural decisions. The number of eggs laid by American 'parasitoids' ranged from 548 to 679, with an average of 630, in these ten sets of simulations. The European 'parasitoids' laid 438-555 eggs, with an average of 503. Most of the simulations with an increase or decrease in a single behavioural parameter value of 10% fell within the above ranges, and did not differ significantly from the default simulation set.

American parasitoids showed a trend for a higher fitness, (759 eggs), when the giving up time on infested leaves was decreased with 10 % ($P=0.0475$), as well as a trend for a higher fitness, (683 eggs), when the probability to go to infested leaves was increased ($P=0.0328$). European parasitoids had a significantly higher fitness (592 eggs) when the giving up time on infested leaves was increased ($P=0.0051$), and a significantly lower fitness (424 eggs) when the probability to revisit infested leaves was decreased ($P=0.019$).

Time limited or egg limited?

Host distribution clearly affected the proportions of time-limited and egg-limited parasitoids in the American and European populations. Of the American parasitoids 83 % was time-limited in the Poisson environment, and 50 % in the negative binomial environment. In comparison, a somewhat larger percentage of the European parasitoids tended to be time-limited. Of the European strain 91 % was time-limited in the Poisson environment, and 61 % in the negative binomial environment. These percentages hold for animals with a fecundity of 1400 eggs. Figure 4 shows how the percentage of time-limitation increased with fecundity in the American parasitoid population, in the Poisson and negative binomial ($NB_{multiple}$) environments (see discussion).

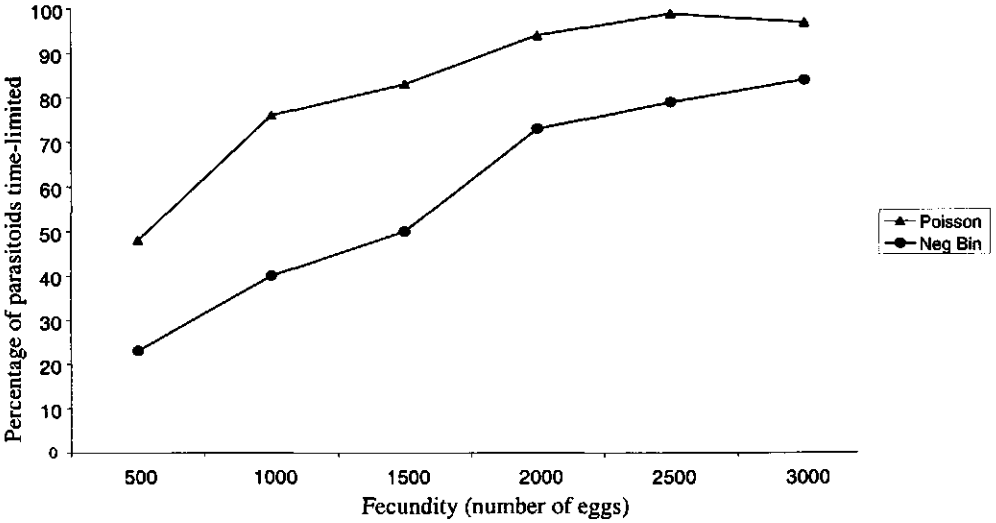

Figure 4 Percentage time-limitation in the American parasitoid population in environments with Poisson and negative binomial ($NB_{multiple}$) distributions of hosts across plants.

The parasitoids of both strains made more visits to empty than to (rare) infested leaves in the Poisson environment. The European strategy led on average to 194 visits to empty leaves versus 84 visits (including revisits) to infested leaves during a parasitoid lifetime (MWU, $P=1.5\cdot10^{-7}$). European parasitoids visited on average 60 different plants, of which up to 30 were infested with *P. rapae*. The American strategy led on average to 105 visits to empty leaves versus 61 visits to infested leaves (including revisits), during a life time (MWU, $P=1.3\cdot10^{-6}$), in the Poisson environment.

The American parasitoids visited less empty leaves than their European conspecifics, in the Poisson environment (MWU, P=0.0050). In the negative binomial environment the parasitoids of both strains visited more infested than empty leaves. The European strategy led on average to 113 visits to infested leaves and 82 visits to empty leaves during a parasitoid lifetime (MWU, P=0.00048). The American strategy resulted in means of 50 visits to infested leaves and 23 visits to empty leaves during a lifetime (MWU, $P=2.2\cdot10^{-12}$).

Variation in life span and fecundity

Figures 5 en 6 show parasitoid reproductive success in a negative binomial ($NB_{multiple}$) and a Poisson environment depending on life span and fecundity, for the American strategy. The increase in reproductive success with life span is about two times steeper in the negative binomial than in the Poisson environment, for all fecundities. The parasitoids that became egg-limited, did so at a younger age in the negative binomial environment. Note that the horizontal series of data points in figure 5 and 6 represent individuals that were egg-limited at the end of their lives, and that the bundle of data points with a positive slope represents individuals that were time-limited at the end of their lives.

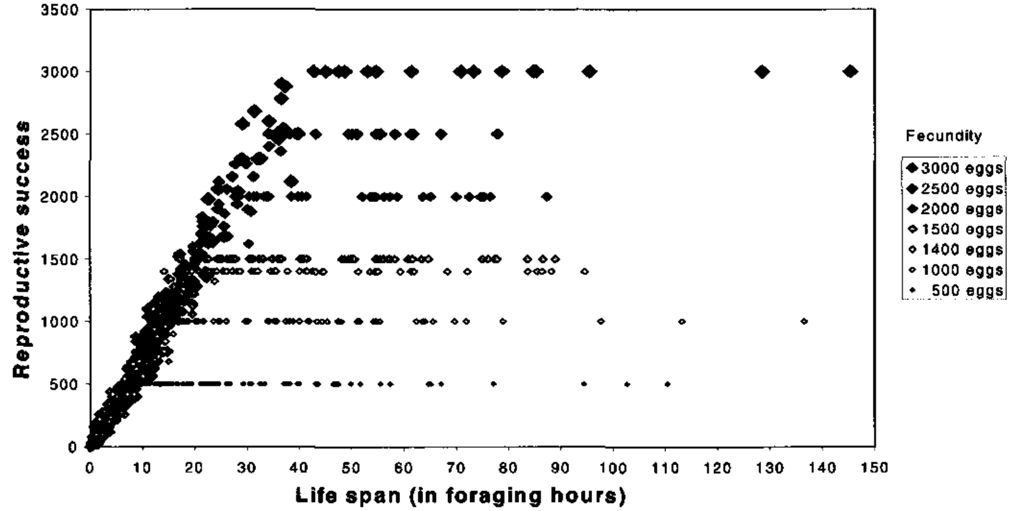

Figure 5 Parasitoid lifetime reproductive success (eggs laid) in a negative binomial ($NB_{multiple}$) environment depending on life span and fecundity, for the American foraging strategy.

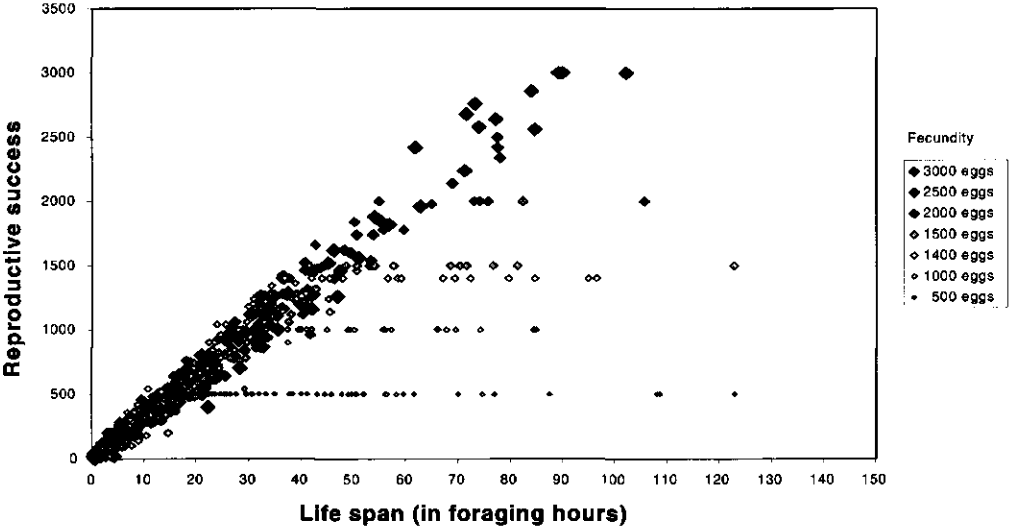

Figure 6 Parasitoid lifetime reproductive success (eggs laid) in a Poisson environment depending on life span and fecundity, for the American foraging strategy.

DISCUSSION

Alternative foraging strategies in *C. glomerata*: adaptive behavioural differentiation?

The foraging strategy of the North American parasitoid population resulted in a higher lifetime reproductive success than the European strategy on a Poisson distribution of hosts across plants. North American *C. glomerata* have to deal with such a host distribution during two periods each year: early on, when the population is building up from the first generation of hosts, and later, during the last host generation that will produce overwintering parasitoids. The North American foraging strategy will result in a higher fitness than the European strategy in the North American environment, where the solitarily feeding host *P. rapae* is present and the gregariously feeding host *P. brassicae* is absent. It would in fact be more efficient in Europe as well, with its Poisson distribution of *P. rapae*, if *P. brassicae* were never present there. Possibly, the European *C. glomerata* foraging strategy is more tuned to investing time and energy in explorative flights in order to increase the chance of encountering rare *P. brassicae* clusters in the European environment (Vos Chapter 4). This explorative behaviour comes at a cost of encountering less *P. rapae* hosts than would be possible under more exploitative foraging behaviour. The European *C. glomerata* strategy may be a compromise between conflicting demands on the behavioural repertoire: Time can be invested in (inefficient) searching on *P. rapae*–infested leaves (see Wiskerke & Vet 1994), or on travelling to locate *P. brassicae.* The parasitoids may risk to miss a high quality cluster of *P. brassicae* when focusing on the exploitation of *P. rapae*, and may risk to have no offspring at all when focusing entirely on rare *P. brassicae* clusters. Host acceptance in *C. glomerata* reflects this compromise: European parasitoids readily accept *P. rapae* after development in this host, but often reject it after development in *P. brassicae*, then only readily accepting *P. brassicae* as a host (Vos Chapter 3). European *C. glomerata* readily accept *P. brassicae*, even when *P. rapae* was the natal host. Interestingly, the American population of *C. glomerata* seems to have lost this trait. It significantly less often accepts *P. brassicae* (Vos Chapter 3). When comparing the behaviour of European and American *C. glomerata*, quite a few traits that are useful for *C. glomerata* when foraging for *P. brassicae* (see Wiskerke & Vet 1994) are absent or less frequent in the North American foraging strategy (Vos Chapter 4). Behavioural differentiation of populations seems to occur more frequently through the loss of (parts of) a behavioural repertoire than through the genesis of novel behaviour patterns (Foster 1999). For example, in a study of more than 25 populations of sticklebacks, all adaptive behavioural differentiation appears to have occurred by loss of ancestral behaviour patterns, or by shifts in the frequency of their expression (Foster 1999). A specific pattern in ecotypic differentiation by loss of behaviour patterns was repeatedly observed, in ten populations in geographically disparate lakes (Foster 1999). We think that the absence of *P. brassicae* in North America may have resulted in resolving part of a conflict within the generalist behavioural repertoire of *C. glomerata*. The current American spatial foraging strategy is certainly more adaptive in this environment. On the Poisson distribution of both on early and late host generations its performance is superior to that of the European strategy. The differences between the European and American strains may reflect genetic differentiation due to 350 generations of selection against traits for dealing with a highly clustered host, in the American environment. However, we cannot exclude maternal effects, although these may have been purged in the laboratory (see materials & methods), nor can we formally exclude potential infections with microorganisms as a cause of the differences between strains (see Hopper *et al.* 1993). Crosses could provide a reliable method to determine the genetic contribution to behavioural variation between strains (Hopper *et al.* 1993). Very little is known about behavioural variation among *C. glomerata* strains within Europe and North America. A North American *C. glomerata* strain from Amherst, Massachusetts, showed flight behaviour that was highly similar to that of our New York strain (Vos Chapter 4), but this strain was less active within patches. Van Nouhuys and Via (1999) showed behavioural differentiation between New York *C. glomerata* strains from wild and cultivated habitats, but could not show local adaptation to these different environments. To our knowledge no behavioural comparison has been made among European *C. glomerata* populations.

Host distribution and adaptation under incomplete information

Previous experiments in a semi-field set-up showed that *C. glomerata* did not change their time allocation to an empty or low density *P. rapae* patch, when an alternative high quality patch with a *P. brassicae* cluster was available at a distance of only 60 cm (Vos Chapter 4). This result indicates that patch leaving decisions are made locally and are not affected by information from nearby patches. It also suggests that the typical hovering across plants and leaves in European *C. glomerata*'s is essential for the location of *P. brassicae*. In our simulations in a Poisson environment, European *C. glomerata* visited 60 different plants in a lifetime, of which up to 30 were *Pieris*-infested. About ten percent of the European parasitoids visited more than 20 different

Pieris-infested plants and would thus have a high probability of encountering a *P. brassicae* cluster during a lifetime.

However, *C. glomerata* are not only attracted to *Pieris*-infested *Brassica* plants in the field. Plant volatiles induced by non-host herbivores confuse these parasitoids and attract them to plants and leaves without hosts (Geervliet *et al.* 1996; Vos *et al.* 2001). Although the parasitoids do not discriminate between host and non-host-infested plants from a distance, they clearly do discriminate between patch types once they have landed on a leaf, and adjust their patch times accordingly (Vos *et al.* 2001). This plant-mediated indirect effect of non-hosts still costs considerable amounts of time, especially when non-hosts are abundant (Vos *et al.* 2001). In a field situation, where multiple-herbivore-plant complexes will be the norm, the distribution of non-hosts may be as important for lifetime reproductive success as the distribution of hosts.

C. glomerata does not use information on the concentration of kairomones in a patch to adjust its leaving tendency (Vos *et al.* 1998). However, the parasitoids might be able to use olfactory information on feeding damage from a distance, and preferentially land on patches with high damage levels (see Geervliet *et al.* 1998, shown for *P. brassicae*, not for *P. rapae*). Our simulations did not show a fitness advantage of a preference for landing on relatively high-density patches. This could easily come as a surprise, if one associates high host densities with high patch quality, high within patch efficiency, and shorter times spent travelling than in a scenario with visits to infested patches of random density. However, *C. glomerata* exploits patches in a way that results in similar efficiencies on densities of one to four hosts on a leaf (Vos *et al.* 1998). Furthermore, travel times between leaves are relatively short, and intervals between ovipositions relatively long. This results in similar efficiencies for scenarios with and without use of information on host densities.

The presence of the clustered high quality host *P. brassicae* may be the main uncertainty in the life of a European *C. glomerata* parasitoid. If a female *C. glomerata* encounters this host early in life, she may learn to specialise on it (Geervliet *et al.* 1998; but see Vos Chapter 3), and use her entire egg complement on one to three clusters of larvae. This is likely to occur when *P. brassicae* is present at peak densities as e.g. in 1982 (see Pak *et al.* 1989). In most years only a minority of *C. glomerata* is likely to encounter a single cluster of *P. brassicae*, probably after spending quite a lot of time on *P. rapae* (or even non-host) patches. Of course the above uncertainty does not play a role in North America because *P. brassicae* is consistently absent there.

Distribution as a host strategy

Our simulations showed that lifetime reproductive success in North American *C. glomerata* would be lower in a negative binomial environment, if adult *P. rapae* butterflies decided to always only lay single eggs on clean leaves. Under the *P. rapae* distribution that would result from such behaviour, the risk of parasitism would be lower for individual larvae. In fact, *P. rapae* butterflies do tend to lay single eggs on leaves, on the leeward side of plants (Harcourt 1961). However, egg laying decisions may be constrained by flight ability, especially in a windy environment (see Harcourt 1962). Butterflies may experience only a few leaves on each plant as suitable for landing, and thus separate females will tend to lay single eggs on the same leaves. This can result in a situation where plants may have only one or two infested leaves, each containing 5 larvae (S. van Nouhuys pers comm). *P. rapae* will face higher parasitization rates in such a distribution.

Time limited or egg limited?

The European strategy will lead to a high proportion of time-limited parasitoids in an environment with a Poisson distribution of *P. rapae* hosts: The majority of female parasitoids will have eggs in their ovaries at the end of their lives. However, in the European environment some parasitoids will have a chance to find *P. brassicae*. They could easily lay their remaining egg complement in a single cluster of this host and thus achieve a relatively high contribution of offspring to the next generation (see Driessen & Hemerik 1992; Ellers 1998; Ellers *et al.* 2000, for parallel parasitoid systems). As mentioned above, time limitation may not only depend on the temporal and spatial distribution of the host species *P. rapae* and *P. brassicae*, but also on the distribution of non-host herbivores that cause *C. glomerata* to waste time. The American situation is interesting, in that host generations follow an alternation of Poisson and negative binomial distributions. Parasitoids are selected to have (relatively) many eggs in the negative binomial environment, but their offspring will emerge in a Poisson environment where it would have paid to invest in longevity. Such changing selection pressures in subsequent generations may lead to the evolution of a trade-off that is not optimal in any of the two environments.

It would be interesting to compare *C. glomerata* from northern and southern populations. In more southerly areas, a longer growing season supports more generations per year (e.g. six occur around Colombia, Missouri) (http://eap.mcgill.ca/CPC_1.htm). In southern populations selection may lead to higher investments in fecundity than in northern populations.

General conclusions

Host distribution has a significant effect on parasitoid lifetime reproductive success. Natural selection may lead to striking geographic variation in foraging behaviour on different host distributions, within a period of 350 parasitoid generations. Constraints on the informational state of individual parasitoids are unimportant with respect to some aspects of environmental variation, but do matter with respect to other environmental characteristics. We showed that the parasitoids' foraging strategy was robust to a lack of information on host densities, and to the fact that information is only locally available. A lack of information on the presence of the preferred host *P. brassicae* in Europe may be much more important: The European strategy seems a compromise in which explorative efforts to locate *P. brassicae* cause a reduced efficiency in the exploitation of *P. rapae*. American *C. glomerata* do not face this dilemma, and seem to have adapted to the American *P. rapae* environment by spending their time and energy on exploitation, and not on the costly explorative behaviour that is so characteristic of their European conspecifics.

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Appendix

C. glomerata parasitoids adjust their tendency to stay searching in a patch with each oviposition they have (Vos *et al.* 1998). This means that realised patch residence times and efficiencies depend both on the parasitoids' 'intrinsic tendency' to encounter hosts, and on the parasitoids' intrinsic tendency to leave (1/GUT). In the model the occurrence of ovipositions during a patch visit depends on draws from two variables that represent these intrinsic tendencies. For convenience we call these: the intrinsic interval between ovipositions (IBO) and the intrinsic giving up time (GUT). We calculated the intrinsic IBOs and GUTs from the realised IBOs and GUTs that we observed in our experiments. Note that the realised experimental values are not identical to these underlying variables. For example, if the average intrinsic GUT were small relative to the underlying IBO, the IBOs observed in the experiment would only represent the leftmost tail of the distribution of IBOs (because parasitoids mostly leave a patch before the underlying IBO has a chance to become realised). Below we provide a technical description of our method to determine these underlying processes that wil result in realised intervals between ovipositions and giving up times:

Realised IBOs and GUTs result from two underlying random processes with different mean times of occurrences. These processes are assumed to be generating theoretical values for IBOs and GUTs following exponential distributions with parameter λ_1 and λ_2 respectively. For a stochastic variable, say Z, following an exponential distribution with parameter λ, the mean and variance are $1/\lambda$ and $(1/\lambda)^2$ (see A1 for the cumulative distribution function).

$$\text{(A1)}\quad F(z) = P(Z \le z) = \int_0^z \lambda e^{-\lambda t} dt$$

The realised intervals between ovipositions are the cases for which the stochastic variable Y (giving up time) has a value T_{gut} that is greater than the value T_{ov} for the stochastic variable X (inter-oviposition time). The realised IBOs and GUTs have, theoretically, means given by the conditional expectations $\mathbf{E}(X|Y \ge X)$ and $\mathbf{E}(Y|X \ge Y)$. It can easily be shown that both these conditional expectations have the same value. The starting integral, some intermediate results and the expected value are given for the realised IBOs in (A2).

$$\text{(A2) } \mathrm{E}(X|Y \geq X) = \frac{\int_0^\infty \int_0^y x\lambda_1 e^{-\lambda_1 x} \lambda_2 e^{-\lambda_2 y} dx \cdot dy}{\int_0^\infty \int_x^\infty \lambda_1 e^{-\lambda_1 x} \cdot \lambda_2 e^{-\lambda_2 y} dy \cdot dx} = \frac{\lambda_1 / (\lambda_1 + \lambda_2)^2}{\lambda_1 / (\lambda_1 + \lambda_2)} = \frac{1}{\lambda_1 + \lambda_2}$$

From our experiments we computed the observed mean value for all IBOs and GUTs. This represents the realised value of $1/(\lambda_1+\lambda_2)$. Before we were able to estimate the mean values for the theoretical distributions $1/\lambda_1$ and $1/\lambda_2$, it was necessary to look at the fraction of the observations that is a realised giving up time. The complementary fraction is the fraction of realised intervals between ovipositions. In (A3) it can be seen that the fraction of realised ovipositions in the data equals $\lambda_1/(\lambda_1+\lambda_2)$. Therefore, we estimated $1/\lambda_1$ as the quotient of the observed mean time for both GUTs and IBOs and the fraction of realised ovipositions.

$$\text{(A3) } P(Y \geq X) = \int_0^\infty \int_x^\infty \lambda_1 e^{-\lambda_1 x} \cdot \lambda_2 e^{-\lambda_2 y} dy \cdot dx = \frac{\lambda_1}{\lambda_1 + \lambda_2} = 1 - P(X \geq Y)$$

The results of this calculation are presented in table 3.

Table 3 Data from behavioural records necessary for the calculation of the theoretical mean $1/\lambda_1$ for intervals between ovipositions (IBO) and $1/\lambda_2$ for giving up times (GUT).

	$N_{observed}$ IBO	$N_{observed}$ GUT	Fraction obs. inter-ovip	Fraction obs. GUT	Total mean (s)	Estimated $1/\lambda_1$ (s)	Estimated $1/\lambda_2$ (s)
Am	72	60	0.56	0.44	376	671	855
Eur	39	89	0.30	0.70	271	903	387

6

Plant-mediated indirect effects and the persistence of parasitoid-herbivore communities

Summary

We have examined the effects of herbivore diversity on parasitoid community persistence and stability, mediated by non-specific information from herbivore-infested plants.

First, we investigated host location and patch time allocation in the parasitoid *Cotesia glomerata* in environments where host and/or non-host herbivores were present on *Brassica oleracea* leaves. Parasitoids were attracted by infochemicals from leaves containing non-host herbivores. They spent considerable amounts of time on such leaves. Thus, when information from the plant is indistinct, herbivore diversity is likely to weaken interaction strengths between parasitoids and hosts. In four *B. oleracea* fields, all plants contained herbivores, mostly two or more species. We modelled parasitoid-herbivore communities increasing in complexity, based on our experiments and field data. Increasing herbivore diversity promoted the persistence of parasitoid communities. However, at a higher threshold of herbivore diversity parasitoids became extinct due to insufficient parasitism rates. Thus, diversity can potentially drive both persistence and extinctions.

INTRODUCTION

Infochemicals play a key role in multi-trophic relationships, mediating direct and indirect interactions (Vet & Dicke 1992; Dicke &Vet 1999; Stowe *et al.* 1995; Sabelis *et al.* 1999). The information web, based on infochemicals, is more complex than the food web (Dicke & Vet

1999; Vet 1999). Any infochemical can potentially be used in the battle between consumers and resources, either for defences, or for attacks. Many parasitoids and predators of insect herbivores use volatiles from herbivore-infested plants for the long-distance location of their victims (Vet & Dicke 1992). Some plants can emit specific volatile blends for different herbivore species (De Moraes *et al.* 1998) and thus selectively attract parasitoids (Du *et al.*1996; De Moraes *et al.* 1998). However, several parasitoid species are attracted to plants and leaves infested with non-host herbivores (Agelopoulos & Keller 1994; Geervliet *et al.* 1996). The volatile blends from these plants may be non-specific or very similar for different herbivore species. The above studies have considered the response of parasitoids or predators to plants infested with only one herbivore species. The study by Shiojiri *et al.* (2000) is an interesting exception. It compares attraction to plants with hosts alone versus the combination of host and non-host species. The majority of plant species in the field will be attacked by a complex of herbivores (Lawton & Schröder 1978; Futuyma & Gould 1979; Futuyma 1983). Natural enemies will often have to choose between plants containing a complex of host and non-host herbivores versus plants infested with non-hosts only. This is exactly the topic of the present paper. As yet there are no studies available on the volatile blends produced by plants infested with a complex of herbivore species. It is likely though that such blends are more difficult to 'interpret' for natural enemies. It is still unknown whether plant species that attract a particular parasitoid species when attacked by one herbivore species, are still able to do so when infested with a complex of herbivores.

Recent advances in the diversity-stability debate have not taken into account that many trophic interactions are mediated by infochemicals (e.g. McCann *et al.* 1998; see McCann 2000 for a review; Borrvall *et al.* 2000). These contributions are important in that they reconnect ecological theory with the brimming complexity of real communities (Polis 1998). They show that species diversity can increase food web stability, when weak trophic links dampen the oscillations of strong consumer-resource interactions (McCann *et al.* 1998; McCann 2000). Smaller fluctuations reduce the probability of extinctions, thus promoting food web persistence. In addition, Borrvall *et al.*'s (2000) model suggests that high-diversity food webs are less prone to cascading extinctions than low-diversity ones, should a single species be lost.

We are interested in the effect of herbivore diversity on the use of plant information by parasitoids. Is plant information less informative in a multiple-herbivore environment, and does this weaken potentially strong parasitoid-host interactions? A major question is whether we should expect such a majority of weak links to evolve (also see Kokkoris *et al.*1999) if interaction strengths in natural communities are indeed skewed towards weak ones (Paine 1992; Raffaelli & Hall 1996), and if models predict that such weak links are important for food web persistence (McCann *et al.* 1998). We investigate field data on herbivore species diversity on the single plant species *Brassica oleracea.* In laboratory experiments we examine whether parasitoids are constrained in their discrimination between leaves infested with hosts, non-hosts, and complexes of host and non-host herbivores. The parasitoids waste valuable time on leaves containing only non-host herbivores. Based on these results we explore models of parasitoid-herbivore communities that occur on a single plant species. In contrast with the study by McCann *et al.* (1998), we investigate communities in which infochemical-mediated interactions directly weaken strong consumer-resource interactions. This mechanism is qualitatively different from a weak trophic interaction dampening a strong one, as it acts through information links instead of trophic links. We hypothesise that increasing diversity at the herbivore level will initially increase the persistence of the parasitoid community. Parasitoid extinctions at high levels of herbivore diversity are, however, to be expected. At such high levels of diversity the parasitoids can become so inefficient, that their reproduction does not compensate for mortality.

In nature, plants may vary considerably in the specificity of the volatile information they provide. Parasitoid species may differ in their ability to discriminate between highly similar odour blends, or in the time they waste on leaves with non-host herbivores. Within parasitoid species, individuals may vary because of species-specific genetic variation and/or learning. A major question is how natural selection will act on such variation. To study the effect on the community we allow the different parasitoid species in our model to be affected in varying degrees by non-host herbivores.

Our analysis indicates that indirect interactions in the information web can exert major effects on food web persistence and need to be incorporated in the diversity-stability debate. The entire complex of non-host herbivores can determine the interaction strength between a herbivore and its parasitoid. In that sense different herbivore species are not 'redundant'. Every single species in a diverse community contributes to the probabilities of persistence and extinction in that community.

METHODS

Field samples

In four pesticide-free fields (each 37 x 42 m), close to Wageningen, the Netherlands, with Brussels sprouts plants, *Brassica oleracea gemmifera* cv. Icarus, whole plants were sampled for the presence of insect herbivores. One sample consisted of a block of 5 x 5 plants. Five samples were taken within one week (125 plants, 4824 leaves).

Behavioural assays

Parasitoids originated from cabbage fields in the vicinity of Wageningen and were collected during the previous season. Female parasitoids of the species *Cotesia glomerata* were used (three to five days old). Experimental plants, *B. oleracea* (of the above variety) were three months old. The host and non-host herbivores used in bioassays were the preferred first instar *Pieris rapae* (*P.r.*) larvae and late third and early fourth instar *Plutella xylostella* (*P.x.*) larvae. Experiments were carried out in a greenhouse compartment at 22-26 °C, 60-70% RH.

Experiment 1, dual choice set-up.

Two fans behind a gauze provided air flow at a distance of 80 cm from the two odour sources *i.e.* individual Brussels sprouts leaves, placed in a 500 ml Erlenmeyer filled with water and plugged with cotton wool. The parasitoid release site and odour sources formed an equilateral triangle with 40-cm sides. Wind speed was 0.3-0.35 m/sec in experiment (1a), and was reduced to 0.20-0.25 m/sec in experiment (1b), which increased parasitoid responsiveness. The landing choice of individual parasitoids was tested for several combinations of herbivore-infested leaves, similar to those occurring in the field. Experiment (1a): 6 (*P.x.*) *versus* 2 (*P.r.*). Experiment ($1b_1$): clean *versus* 2 (*P.r.*) and, ($1b_2$): 6 (*P.x.*) *versus* 2 (*P.r.*) and 6 (*P.x.*). Infestation was obtained by allowing larvae of *P. xylostella* and/or *P. rapae* to feed on a single leaf on a plant for about 24 hours before testing. Leaves were cut off the plant just prior to experiments. Release sites for parasitoids were prepared in a similar way. Before each test, the caterpillar was removed, and the leaf area containing frass and damage due to 1 (*P. r.*) was cut out, to be used as release site. At the start of each choice test, a parasitoid was placed on the release site to give it experience with odours associated with its host. After each test, left and right odour sources were exchanged.

Replicates experiment (1a): 26 parasitoids were tested in 7 days. Replicates experiment (1b): 70 parasitoids were tested in ($1b_1$) and 79 in ($1b_2$) over the course of 16 days.

Experiment 2, patch leaving decisions.

We observed leaf departure on a single leaf of an experimental plant that was placed in front of six infested plants that simulated a background natural environment. At the end of the set-up two fans provided an air current. The distance between plants was about 30 cm. At the experimental leaf wind speed was 0.2-0.25 m/sec. Treatments: Three of the background plants were infested with six (*P. x*). The other three plants were infested with two (*P. r.*) and six (*P. x.*). The two types of plants had alternating positions within and between the two rows. An experimental leaf was either: (i) a clean leaf on a clean plant; (ii) the only infested leaf on a plant with 6 (*P.x.*); or (iii) the only infested leaf on a plant with 6 (*P.x.*) and 2 (*P.r.*). The larvae were carefully placed on the plants about 24 hours in advance of the experiments. Before each test, a parasitoid was given experience on the same type of leaf disc as in experiment 1, for a period of three minutes. Behaviour was recorded using a handheld computer, until a parasitoid flew away and landed somewhere else or remained motionless for more than five minutes. Replicates experiment 2: For each of the 3 treatments 21 parasitoids were observed. Statistical analysis: Experiments (1a) and (1b) were analysed with a generalised linear model (GLM), in SAS 6.11. The results of choices on a single day were taken as a single replicate. Experiments (1b1) and (1b2) were compared using a GLM as well. Experiment 2 was analysed with a Kruskal-Wallis test and non-parametric multiple comparisons (mc), (Siegel & Castellan 1988).

The model

We investigate how the diversity of herbivores and parasitoids, under incomplete plant information, affects variability, both at the level of the population and the entire community. In particular we study whether diversity bounds the minima during population fluctuations away from zero, (and above one). In addition we study how diversity, and the extent to which parasitoids are constrained by incomplete information, affect parasitoid community persistence and extinctions. Our approach is to compare ecological scenarios. We start with a simple community consisting of a single herbivore and its specialist parasitoid. Then we proceed by analysing communities of increasing complexity by adding parasitoid-host pairs. Our model describes the interaction of up to eight competing herbivores (H_i, i=1, ...,8), with up to eight specialist parasitoids (P_i, i=1, ...,8) and is a modified and extended version of the Rosenzweig-MacArthur equations (Rosenzweig & MacArthur 1963) and the model by Kretzschmar *et al.* (1993). Each herbivorous host can grow to carrying capacity following logistic growth. The carrying capacity of each host is decreased due to inter-specific competition. Each parasitoid species wastes some of its time on non-host herbivores. This is incorporated as parameter *f* in the parasitoids' Holling type II functional response (Holling 1959). This parameter represents the time spent on non-hosts as a fraction of the time spent on hosts. As the number of herbivore species in the community increases, the interaction strength between each parasitoid and its host decreases, as each added non-host herbivore further reduces effective search time.

For simplicity and clarity we give each parasitoid and host species identical biological parameter values, except parameter *f* in the parasitoids. We analyse the model for scenarios where parasitoid species differ in the amount of time they waste on non-host herbivores. As an example we present a community with seven parasitoid-host pairs, where the *f*–values are 0, 0.1, 0.12, 0.14, 0.16, 0.4, and 0.6. We assume plants to be present throughout the parasitoid-host interaction. The model has *n* parasitoid-host pairs, with (n = 1,...,8). Hence there are 2*n* differential equations (i=1,...,8):

$$\frac{dH_i}{dt} = r \cdot H_i \cdot \left(1 - \frac{H_i}{k} - \frac{w}{k} \cdot \sum_{\substack{j=1 \\ j \neq i}}^{n} H_j \right) - \frac{P_i \cdot x \cdot H_i}{z + H_i + f \cdot \sum_{\substack{j=1 \\ j \neq i}}^{n} H_j}$$

$$\frac{dP_i}{dt} = \frac{c \cdot P_i \cdot x \cdot H_i}{z + H_i + f \cdot \sum_{\substack{j=1 \\ j \neq i}}^{n} H_j} - \mu \cdot P_i$$

where r denotes maximum relative growth rate of herbivores, k the carrying capacity of herbivores, w the coefficient of competition between herbivores, x the attack rate of parasitoids, z the half saturation constant, f the time wasted on non-hosts as a fraction of the time spent on hosts, c the conversion of herbivores into parasitoids, by parasitism, and μ the death rate of parasitoids. Initial population densities of herbivore species 1-8 are 996, 997, ...,1003 and of parasitoids 1-8 are 96, 97,...,103. Parameter values are given in the figure captions. The conclusions based on this model are robust for a simultaneous increase or decrease of all parameter values with 10 or 30%. Individual parameter values were increased or decreased with 50%. This resulted in essentially the same pattern as in Figures 1 and 2, but shifted left, right, up, or down, relative to the same increase in community complexity. We used a numerical integrator (GRIND, De Boer (1983)) that implements a variable time-step method, ROW4A (Gottwald & Wanner1981).

RESULTS

Field samples

In our samples from four *Brassica oleracea* fields, all plants were herbivore-infested, with 73 % of the plants containing two or more herbivore species. Plants were infested with aphids, mainly *Brevicoryne brassicae*, and some *Myzus persicae*, with *Phyllotreta* leaf beetles, and with the caterpillar herbivores *Plutella xylostella*, *Autographa gamma*, *Mamestra brassicae* and *Pieris rapae*, a host of the parasitoid *Cotesia glomerata*. The different herbivore species frequently co-occurred on a single leaf.

Experiment 1

We focused on the parasitoid *C. glomerata*, a host species *P. rapae*, and a non-host species *P. xylostella* in our laboratory bioassays. In a dual choice flight set-up, *C. glomerata* parasitoids did not discriminate between leaves infested with their host *P. rapae* and leaves infested with the non-host *P. xylostella* (GLM, P=0.70, $n_{days}=7$, $n_{wasps}=26$, Table 1, exp. 1a). In experiment (1b) the parasitoids showed clear discrimination between leaves infested with the host *P. rapae* and uninfested leaves (GLM, P=0.0001, $n_{days}=15$, $n_{wasps}=59$). In 86% of the cases parasitoids chose for the host-infested leaf (Table 1).

Table 1 Number of landings of the parasitoid *C. glomerata* in dual choice tests between differently infested cabbage leaves. Clean represents undamaged leaves. Infested leaves contain the non-host herbivore *P. xylostella* and/or the host herbivore *P. rapae.*

Dual choice test		Landings	Percentage To host-leaf	P-value
(1a)	non-host *vs.* host	12 vs. 14	54 %	0.70
($1b_1$)	clean *vs.* host	8 vs. 51	86 %	0.0001 *
($1b_2$)	non-host *vs.* non-host + host	27 vs. 42	61 %	0.062
GLM-test for difference in choices between ($1b_1$) and ($1b_2$)				0.0019 *

The percentage of *C. glomerata* females choosing for the leaf containing the host significantly dropped when non-host larvae were present on both odour sources (GLM, P=0.0019, Table 1). Only 61% of the parasitoids made a choice for the leaf that contained the host in this set-up (Table 1). This is not significantly different from random (GLM, P=0.062, n_{days}=15, n_{wasps}=69).

Experiment 2

Patch residence times on leaves with non-host herbivores (and on clean leaves) were on average about 400 seconds. This is significantly different from the 900 seconds on leaves where both host and non-host larvae were present (mc, P=0.006; mc, P=0.002 respectively).

The model

In our model, a single parasitoid species and its host have a strong interaction, experiencing fluctuations that would effectively lead to the extinction of the parasitoid (Figs. 1 and 2). Without plant-mediated indirect links between parasitoids and non-host herbivores, more complex parasitoid communities would experience the same non-viable minimum number during fluctuations. However, if each parasitoid experiences a weak negative indirect effect of all non-host herbivore species in the system, increasing complexity does decrease the amplitude of oscillations and keeps parasitoid population densities further away from zero (Figs. 1 and 2, *f*=0.1).

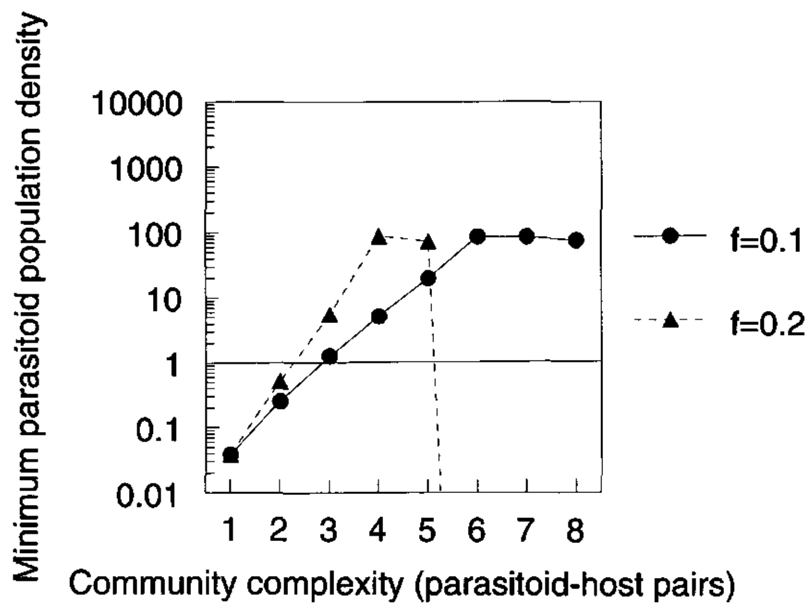

Figure 1 Minimum parasitoid population densities in parasitoid-host communities of increasing complexity, for *f*=0.1 and *f*=0.2 ($r = 0.09$; $k = 10000$; $w = 0.1$; $x = 0.2$; $z = 1000$; $c = 1$; $\mu = 0.1$).

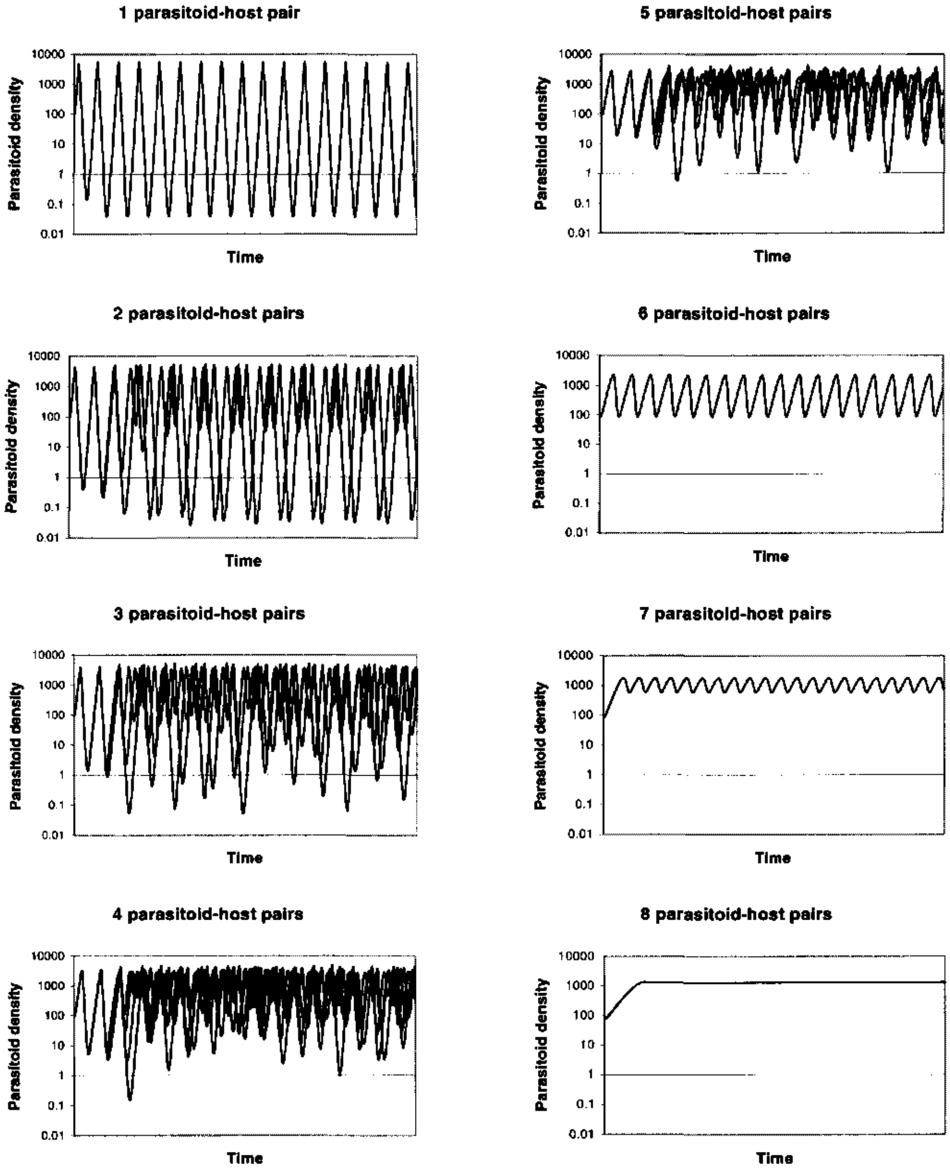

Figure 2 Parasitoid dynamics in communities of increasing complexity, f=0.1 ($r = 0.09$; $k = 10000$; $w = 0.1$; $x = 0.2$; $z = 1000$; $c = 1$; $\mu = 0.1$).

Herbivore densities exhibit a similar pattern (not shown). In this example, with *f* = 0.1, the community shows several qualitative shifts in its dynamics: three, four or five parasitoid species show irregular fluctuations, six or seven parasitoid species exhibit limit cycles, and eight different parasitoids converge to a stable equilibrium. The dynamics of the community become more reliable as diversity increases. However, if we increase the indirect effect of non-host species, (by increasing parameter *f* from 0.1 to 0.2, e.g. because parasitoids waste a lot of time on non-hosts), the parasitoids in complex communities can become so inefficient that they go extinct (Fig. 1). For *f*=0.2 dynamics stabilise at five pairs, but all parasitoid population densities decrease exponentially in communities with six or more parasitoid and herbivore species. In that case all herbivores grow to their carrying capacity.

In the above analyses all parasitoids were given an equal *f*-value, for time wasted on non-hosts. In nature, each parasitoid species may have a certain range of *f*-values, because of species-specific genetic variation and/or learning. As we are interested in the role of natural selection in shaping communities, we also allowed the different parasitoid species to be affected in varying degrees by non-host herbivores. We observed that populations of parasitoids that waste a lot of time on non-hosts, i.e. with high *f*-values (0.4, 0.6) went extinct (Fig. 3). The population with *f*=0 exhibited large oscillations, with minimum population densities below one.

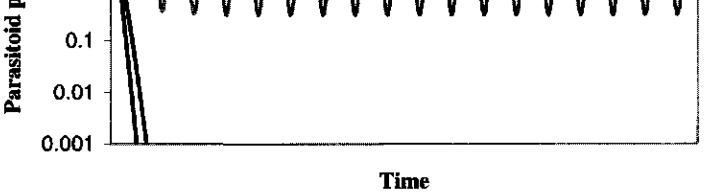

Figure 3 Parasitoid dynamics, each species with a different *f*-value (for time wasted on non-host herbivores). *f*=0: large fluctuations, *f*=0.1-0.16: limit cycles far away from zero, *f*= 0.4, 0.6: extinct.

From a practical point of view this indicates extinction as well. The remaining parasitoid populations had low to intermediate *f*-values (0.1-0.16). These populations exhibited limit cycles with minimum densities far above one.

DISCUSSION

Strong consumer-resource interactions are weakened by diversity at the level of resource species, if this diversity causes consumers to waste time. The time spent handling non-diet resources lowers the maximum consumption rate of a consumer, or, in other words, the plateau of its functional response curve (see e.g. Hughes 1979; Kretzschmar *et al.*1993). In addition, 'wasted time' tends to weaken the relative effect of host density in the denominator of the functional response equation. This reduces the destabilising effect of inverse density dependence under a Type II functional response (see e.g. DeAngelis *et al.* 1975; Murdoch & Oaten 1975; Crawley 1992). We can think of many interactions where resource diversity imposes time costs on consumers. Of course such costs will mainly have an impact on consumers that are time-limited. In any system where consumers need a recognition time in order to discriminate between diet and non-diet items, increased diversity will weaken consumer-resource interaction strengths. This holds true because each and every consumer species needs to deal with an increasing proportion of non-diet items as resource diversity increases. One can for example think of zooplankton species filter-feeding in water with edible and inedible species of algae (e.g. Kerfoot *et al.* 1985; Kretzschmar *et al.* 1993), sit-and-wait predators handling prey and non-prey species, and parasitoids or predators searching on patches with either diet or non-diet species. 'Wasting time' may be a quite general phenomenon in the biology of animals, with other examples including mutual interference between predators (e.g. DeAngelis *et al.*1975; Hassell 1978; Clark *et al.* 1999), parasitoids being attracted to plant species that never contain hosts (e.g. Takabayashi *et al.* 1998) and prey that stay in a refuge without feeding there (e.g. Gelwick 2000).

Herbivore species co-occurring on a single plant species might be competitors in terms of the food web, but mutualists in terms of the information web. If herbivore complexes make plant information less informative, each herbivore in such a complex might be relatively protected from specialist natural enemies, and, to a lesser extent, from generalists. Our experimental data clearly show that the parasitoids have no problem locating leaves with hosts, if non-hosts are absent. However, this ability was significantly reduced in the presence of non-host herbivores. Most of the literature on volatiles from herbivore-infested plants considers these plant synomones to guide natural enemies to their herbivorous victims and thus solve the reliability-detectability problem (Vet *et al.* 1991; Vet & Dicke 1992). We argue that this view may be too optimistic on the reliability side of it. Complexes of herbivores on a single plant species are common, if not the norm in nature. Such complexes are likely to induce the production of less informative volatile blends as compared to herbivory by a single herbivore. If herbivore-infested plants are non-specifically signalling 'herbivory', and parasitoids waste time on non-hosts, they could be worse off than under random search. This would be a far cry from the 'short-cut guide to dinner' as synomones are considered in chemical ecology today.

Our model results show that such a reduced information content of plant volatile blends may have profound consequences for the persistence of natural enemies. Initially, an increase in the diversity of herbivore species promoted persistence of parasitoid species. Minimum population densities bounded away from zero, and both the dynamics of populations and the community as a whole became less variable, and thus more reliable. However, for our model communities an upper threshold of diversity existed. Adding a single parasitoid-host pair to a stable community at such a threshold, led to the extinction of all parasitoid species in the community. This is a reflection of the fact that all parasitoid species in those model runs had identical biological parameters. If we allowed for variation in f-values (representing time wasted on non-hosts) between parasitoid species, we always observed the species with high f-values going extinct first. As soon as the community was below the upper threshold of diversity, extinctions would stop. This resulted in communities of intermediate complexity. Parasitoids with an f-value of zero (wasting no time on non-hosts at all) exhibited strong fluctuations, with minimum densities below one. Such perfect parasitoids would therefore go extinct as well. In this scenario the remaining communities contained only parasitoid species that waste relatively little time on non-hosts (low to intermediate f-values). From these results a picture emerges of on the one hand natural selection eliminating parasitoids that cannot deal with the complexity of the system, and on the other hand chance operating on small numbers eliminating parasitoids that are perfectly efficient (i.e. they are wasting no time on non-host herbivores (f=0)).

The 'wasted time' mechanism has its greatest potential effect on the persistence of specialist natural enemies. This is in contrast with McCann's (2000) 'added-weak link' mechanism that works for generalists. McCann *et al.* (1998) predicted that specialist-dominated communities are more variable than generalist-dominated ones. We predict that this will only hold if the 'wasted time' mechanism is not operating. This could be the case when plant information is specific, even under herbivory by a diverse assemblage of herbivores. In addition, natural enemies have to be perfectly able to interpret this information.

The persistence in our models depends on the presence of several resource species. Each resource species contributes proportionally to persistence. This sheds a different light on the issue of redundancy (in the sense of having multiple species in a functional group, e.g. Naeem & Li 1997).

When studying the evolution of parasitoid-host interactions in the context of the diversity in natural food webs, more attention should be devoted to volatile production in natural plants infested with multiple herbivore species. Many of the modules in information webs are linked to plant infochemicals, especially in terrestrial food webs. Plant infochemicals have the potential to mediate a whole suite of trophic interactions, like parasitism or predation, intra-guild predation, exploitative competition between predators or parasitoids, apparent competition, and predation or parasitism by top carnivores or hyper-parasitoids (see Dicke & Vet 1999; Vet 1999). It might well be interesting to investigate the relative effects of information web modules and food web modules on the stability of the entire system. Our results show that a diverse community of herbivores and parasitoids can exist on one single plant species. We suggest that the 'wasted time' mechanism mediated by non-specific plant information, might well contribute to the brimming complexity we see in natural communities containing many more plant species than our single species example. It may be one of the mechanisms that cause natural food webs to mainly consist of weak links.

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7

Summarising Discussion

Evolution since Darwin

In 1883, the year after Darwin died, the parasitoid *Cotesia glomerata* was shipped from Britain to the USA. It was released to control *Pieris rapae* on cabbages, became established in 1884 (Clausen 1956) and has foraged in its new environment ever since. Thus *C. glomerata* became part of an unintended evolutionary field experiment (Le Masurier & Waage 1993). European and North American *C. glomerata* populations have experienced different ecological conditions for about 350 generations. An important aspect differentiating these environments is the spatial distribution of the available host species. In North America, *C. glomerata* mainly uses the solitarily feeding herbivore *P. rapae* as a host. The clustered host *P. brassicae* is absent in the USA. In Europe, both these *Pieris* species are attacked by *C. glomerata*. The foraging strategy of European *C. glomerata* is less efficient on *P. rapae* than the strategy of *C. rubecula*, a specialist parasitoid of this species (Wiskerke & Vet 1994). Interestingly, American *C. glomerata* now have a higher attack rate on *P. rapae* than their British conspecifics, suggesting that *C. glomerata* has adapted to attack this host in North America (Le Masurier & Waage 1993).

My chief objective in this study was to evaluate and explain the observed variation in foraging behaviour between *Cotesia* populations in terms of adaptations, constraints and mechanims. We compared the foraging strategies of different populations in the same environment to study genotypic differences, and manipulated environmental information and early adult experience to study phenotypic variation in parasitoid foraging behaviour.

In the first part of this thesis we examined variation in decisions on patch leaving and host acceptance, with a focus on the effects of environmental information and experiences with hosts. In the second part we studied variation in parasitoid travelling behaviour, using behavioural observations in multi-patch environments and a detailed simulation model. We used our simulations to investigate the fitness consequences of alternative foraging strategies in habitats with different host distributions. In the third part of this thesis we combined experimental results, field data and a simple model, to scale up from parasitoid behaviour and information use to the dynamics of diverse parasitoid-herbivore communities. In the rest of this chapter I summarise the results and discuss parasitoid foraging behaviour in terms of adaptation under incomplete information and its consequences at the level of the communitiy. I close with the general conclusions of this study.

The three major objectives of this research project were to evaluate and understand 1) interspecific variation in information use by *C. glomerata* and *C. rubecula* during patch exploitation, 2) the adaptive significance of behavioural differences between European and North American *C. glomerata* populations and 3) the effects of constrained information use in insect parasitoids at higher levels of ecological organisation.

Interspecific variation

In Europe, both *C. glomerata* and *C. rubecula* accept *P. rapae* as a host. *C. rubecula* specialises on *P. rapae*, but *C. glomerata* prefers *P. brassicae*. These host species differ in their spatial distribution on plants. *P. rapae* larvae feed solitarily on leaves and often have a Poisson distribution across plants. *P. brassicae* larvae feed gregariously on a leaf and have highly variable densities on plants. *P. brassicae* clusters are rare in most years in Europe, but they do sometimes occur in high densities. Naïve *C. rubecula* and *C. glomerata* are attracted to *Pieris*-infested plants, irrespective of the particular species on the plant. The above implies that both parasitoids have to deal with patches containing preferred and less preferred hosts in Europe. This leads to the question how both *Cotesia* species deal with such *Pieris*-infested patches, and which information and experiences are used to make decisions on patch exploitation.

In **Chapter 2** I used statistical modelling to analyse patch leaving tendencies in *C. rubecula* and *C. glomerata* in multi-patch environments that contained the preferred or less preferred host, or a combination of these. *C. rubecula* used a simple strategy. Leaving tendencies were high on leaves that were empty or infested with less preferred hosts, especially in the environment where only *P. brassicae* was present. Thus *C. rubecula* spends a short time in unfavourable parts of the environment and will forage extensively on patches with *P. rapae*. *C. rubecula* did not show to use previous experience to make patch leaving decisions in the current patch. Learning is unlikely to improve foraging performance in an environment where infested plants have a random spatial distribution and hosts mostly occur singly on infested leaves.

C. glomerata used flexible behavioural rules in the environment with the clustered host. Ovipositions affected the leaving tendency on the present patch and during subsequent patch visits. The leaving tendency also changed with the number of visits to host-infested leaves. *C. glomerata* switched to a simple type of rule as used by *C. rubecula* in the environments where only *P. rapae* or both host species were present. This suggests that *C. glomerata* may only use its more flexible behaviour in the years with unusually high densities of *P. brassicae*. One aspect of patch leaving in *C. rubecula* and *C. glomerata* is surprising. The parasitoids did not leave directly after an oviposition in *P. rapae*, even when only a single larva was present. This is a waste of time. In addition we did not observe any use of chemical information on host densities to adjust patch leaving tendencies in these two *Cotesia* species. The parasitoids only showed to discriminate between clean and infested leaves. Such wasteful patch time allocation and limited information use seem to reflect a lack of adaptation to the current spatial distribution of *P. rapae* in Europe. However, the concentration of infochemicals on a leaf may be an unreliable source of information on the actual host density (e.g. due to host removal by predators). A strategy that uses unreliable information to assess patch quality will be inefficient and is thus unlikely to evolve. Given the parasitoid's limited use of information and its tendency to prolong patch visits after ovipositions, the best thing *P. rapae* can do is to occur singly in patches. This will minimise the per capita risk of parasitism, as it causes parasitoids to waste a maximum amount of time. Given these limitations, the specialist *C. rubecula* is still an efficient forager on *P. rapae*, relative to *C. glomerata*. It needs a short time to find *P. rapae* in a patch, which allows it to have short giving up times. Thus it seems to minimise its waste of time. *C. glomerata* needs more time to find *P. rapae* in a patch, which requires longer giving up times. *C. glomerata* is a highly efficient forager on patches with *P. brassicae*. The problem lies in locating these rare clusters. The abundance of *P. rapae* patches may to a certain extent mask the presence of *P. brassicae* clusters, that would be more conspicuous if no other herbivores occurred on plants. These species of parasitoids and hosts are involved in a dynamic game of hide-and seek, and the costs and benefits of behavioural rules may keep changing with each of the evolutionary moves of these players. Parasitoids and hosts may use chemical information for attacks and defenses, and exploit constraints on information use in their antagonists.

A comparison of European and North American *C. glomerata* populations

The three main differences between Europe (including Britain) and the USA have been that 1) the clustered high quality host *P. brassicae* is absent in America, 2) *P. rapae* reaches high densities, and a corresponding negative binomial distribution across plants in the middle of the season in America, while *P. rapae* densities remain much lower in Europe, with a corresponding Poisson distribution across plants and 3) *C. rubecula* is absent in most states in the USA. This change in key characteristics of the environment for the introduced *C. glomerata* population raises several questions. Do American *C. glomerata* still accept *P. brassicae* as a host, after not having dealt with it for 350 generations? Do American *C. glomerata* use spatial foraging strategies that are more efficient when foraging for *P. rapae* than European *C. glomerata*? Which are the mechanisms that underly such adaptive variation? In chapters three, four and five I studied variation in foraging behaviour among European and North American *C. glomerata* populations.

In **Chapter 3** I investigated variation in host acceptance. Parasitoids from different populations were compared after development in the same host species, while phenotypic differences were studied after development in different hosts. When European and US parasitoids were reared and tested on *P. rapae*, they did not show any genotypic difference in acceptance of *P. rapae* as a host. However, when both strains were reared on *P. rapae*, but tested on *P. brassicae*, the American parasitoids significantly more often rejected *P. brassicae* than European parasitoids did. The US animals seem to have lost a great deal of their tendency to parasitise this host, that has not been available in the USA for several hundred generations. European *C. glomerata* rejected *P. rapae* significantly more often after development in *P. brassicae* than after having *P. rapae* as its natal host. These parasitoids may use host-derived infochemicals on their cocoon as a cue to the presence of *P. brassicae* in their environment and use this information to reject *P. rapae*. Most of the European parasitoids readily accepted *P. brassicae* for oviposition, irrespective of their natal host. This conforms with the notion of *P. brassicae* being the preferred host of *C. glomerata* in Europe.

In addition I tested whether a series of ovipositions in the preferred host *P. brassicae* would lead to subsequent rejections of *P. rapae* as a host, in European *C. glomerata*. However, acceptance of *P. rapae* did not after the parasitoids had experienced ovipositions in *P. brassicae* versus *P. rapae*. To use a series of ovipositions as a cue for the presence of *P. brassicae* in the environment, would be a bit of an 'a posteriori' way of dealing with information. If *C. glomerata* lands on a cluster of *P. brassicae*, it can probably deposit its entire egg complement in these preferred hosts. Learning to reject *P. rapae* would become rather irrelevant after such an event. So, oviposition experiences may not be a useful source of information for parasitoids that have to decide whether or not to accept the many *P. rapae* larvae they will most likely encounter before ever coming upon a cluster of their preferred host species.

In the US there has been no selective advantage of focusing on cues specifically related to the presence of *P. brassicae* during host location, of retaining a high acceptance level for *P. brassicae*, or of maintaining behaviour that is efficient in the exploitation of patches with clustered hosts. In North America *C. glomerata* will not experience the heterogeneity in larvae across plants as it may experience in Europe when *P. brassicae* is present.

Experience alters host acceptance of low-ranked hosts, but not of preferred hosts in several parasitoid species (Bjorksten and Hoffmann 1998; Duan & Messing 1999). This effect on the acceptance of only low-ranked hosts was similar in the *Cotesia-Pieris* system: experience due to rearing on a specific host affected acceptance of less preferred *P. rapae* larvae, but not of the preferred host *P. bassicae*. Apparently, acceptance of a high quality host is to some extent 'hardwired' in these systems while acceptance of a less preferred host is flexible, and can serve as a 'backup' under conditions where the best host is not available. Interestingly, this 'hardwired' acceptance of *P. brassicae* seems to have been lost during the 350 generations *C. glomerata* did not have access to this host in North America. Behavioural differentiation between geographically separate populations often seems to occur by the loss of (parts of) behaviour patterns (Foster 1999). Another aspect of *C. glomerata* behaviour that may have differentiated is travelling behaviour, as extensive flights may be required to locate rare clusters of *P. brassicae*.

In **Chapter 4** I studied travel patterns in *C. glomerata* parasitoid strains from Europe and North America, in a multi-patch environment. The European strain hovered in front of more plants, had more and longer inter-plant travel times, a higher proportion of inter-plant travel times, and visited more host-infested leaves than the North American *C. glomerata* strain, in the same environment. The European parasitoids experienced many patches, searching each patch for a short time, while the American parasitoids searched only a few patches thoroughly. The American parasitoids had more ovipositions per patch visit than European parasitoids. These differences in spatial foraging behaviour give the impression of a more explorative strategy in the European parasitoids, and a more exploitative strategy in the North American parasitoids. I hypothesise that the extended inter-plant hovering in European *C. glomerata* is a means to facilitate location of *P. brassicae* in Europe, as volatile information might be easier to perceive or use when hovering in and out of odour plumes. In North America explorative flights may not pay-off, as flight is likely to be costly, both in terms of energy and the risk of mortality, while a benefit in the form of rare high quality host clusters is absent in this environment.

Parasitoids use local information, but the exact extent of 'local' is often unknown. Our second experiment intended to test whether the parasitoids use olfactory information from a nearby patch, while making decisions on the current patch. I showed that there was no measurable effect of a high quality *P. brassicae*-infested patch on the patch leaving tendency in *C. glomerata* parasitoids, (even though it would be highly adaptive to quickly leave a poor patch for a high quality patch only 60 cm away). Preliminary experiments showed that the responsiveness to an infested leaf is highest from a distance of 0-30 cm in *C. glomerata*. This is also the distance at which parasitoids hover across leaves. These results indicate that extended hovering may be an essential feature for locating a nearby cluster of *P. brassicae*. Such inter-plant hovering was most pronounced in European *C. glomerata* that had developed in *P. brassicae*. This suggests that *C. glomerata* may use early experience with *P. brassicae* as a cue to the presence of this preferred host in the environment, and adjusts its searching behaviour accordingly.

The above mentioned results indicate that foraging decisions are primarily based on local information, and that *C. glomerata* parasitoids do not simultaneously process olfactory information from several nearby patches, while making decisions in the current patch. However, *C. glomerata* parasitoids frequently revisited patches after several visits to other patches. This can potentially facilitate information use on a larger spatial scale. Although it is not immediately clear whether revisits result in a higher pay-off than visits to new patches, this result is important from a theoretical point of view: Initial patch leaving decisions as observed within a limited experimental timeframe, may not represent the final decision of a parasitoid for that patch. Patch exploitation can consist of multistage decision making, where initial decisions are adjusted after the parasitoids have dealt with (and maybe learned on) several other patches in the local environment.

In **Chapter 5** I investigated how variation in foraging behaviour between American and European parasitoids affects lifetime reproductive success. A detailed simulation model was used to extrapolate from our experimental results to the lifetime foraging of these parasitoids in environments with different spatial distributions of *P. rapae*. The 'American strategy' resulted in a higher fitness on a Poisson *P. rapae* distribution, which normally occurs in Europe and early and late in the season in North America. Reproductive success did not differ between strategies on the negative binomial distribution, which is characteristic for midsummer American *P. rapae* populations. The 'European strategy' paid for its prolonged explorative flights between plants that could not result in locating a *P. brassicae* cluster in an environment with only *P. rapae*. The 'American strategy' did not waste time on such flights and allocated most of the time to intra-patch searching for *P. rapae*. Lifetime reproductive success of the European foraging strategy was most sensitive to an increase in the giving up time on leaves. The American parasitoids differed most from their European conspecifics in exactly this behavioural parameter and showed a 121% higher GUT.

In the first simulations parasitoids could not discriminate from a distance between different host densities on infested plants and leaves. Following simulations allowed the parasitoids to perceive information on plant and/or leaf damage levels in their local environment, and to use this information to preferentially land on high-density patches. Lifetime reproductive success did not significantly increase under such an increased perception and use of information. This may be due to the fact that the current patch leaving strategy is not tuned to make efficient use of this information on host densities.

In Europe, less than one in every twenty *Pieris*-infested plants has a cluster of *P. brassicae* on it. In the simulations only ten percent of the European parasitoids visited more than twenty *Pieris*-infested plants. This indicates that *C. glomerata*'s probability of encountering a *P. brassicae* cluster during a lifetime in Europe is low, given its current strategy for travelling and patch exploitation.

The simulations showed that lifetime reproductive success in North American *C. glomerata* would be lower in a negative binomial environment, if adult *P. rapae* butterflies decided to always lay single eggs on clean leaves. Under the *P. rapae* distribution that would result from such behaviour, the risk of parasitism would be lower for individual larvae. *P. rapae* butterflies probably do prefer to lay single eggs on clean leaves. However, conditions may be windy, butterfly flight ability constrained and few cabbage leaves suitable for landing. This may result in the higher densities per leaf in North American midsummer *P. rapae* populations.

The variation in foraging behaviour between American and European *C. glomerata* does not reflect a simple change in a single trait. All behavioural parameters for patch arrival, patch leaving and travel time decisions varied considerably between these populations. Differences fell within a range of a 66% decrease to a 121% increase in parameter values. These parasitoids occupy remarkably different areas in behavioural parameter space.

Community-level consequences of incomplete information

In **Chapter 6** I investigated how the presence of nonhost herbivores on plants affects the foraging behaviour of *C. glomerata*, and modelled the potential effects at the level of the community. *C. glomerata* uses herbivore-induced plant volatiles to locate its hosts. Since plants are most likely attacked by a complex of herbivores, I asked how parasitoids deal with plant information that reflects herbivory by both host and nonhost herbivores.

Our experimental results showed that *C. glomerata* faced problems when nonhosts were present in the environment. Parasitoids were attracted by infochemicals from leaves with nonhost herbivores and spent considerable amounts of time on such leaves. When information from the plant is indistinct, herbivore diversity is likely to weaken interaction strengths between hosts and specialist parasitoids. The model results showed that small increases in herbivore diversity promoted the persistence of parasitoid communities. However, at a higher threshold of diversity parasitoids became extinct due to insufficient parasitism rates. Thus diversity can potentially drive both persistence and extinctions, if diversity causes parasitoids to waste time. 'Wasting time' may be a quite general phenomenon in the biology of animals, with other examples including mutual interference between predators (e.g. DeAngelis *et al.*1975; Hassell 1978; Clark *et al.* 1999), parasitoids being attracted to plant species that never contain hosts (e.g. Takabayashi *et al.* 1998) and prey that stay in a refuge where they are unable to feed (e.g. Gelwick 2000).

Herbivore species co-occurring on a single plant species might be competitors in terms of the food web, but mutualists in terms of the information web. If herbivore complexes make plant information less informative, each herbivore in such a complex might be relatively protected from specialist natural enemies, and, to a lesser extent, from generalists. My experimental data clearly show that the parasitoids have no problem locating leaves with hosts, if non-hosts are absent. However, this ability was significantly reduced in the presence of non-host herbivores. Most of the literature on volatiles from herbivore-infested plants considers these plant synomones to guide natural enemies to their herbivorous victims and thus solve the reliability-detectability problem (Vet *et al.* 1991; Vet & Dicke 1992). I argue that this view may be too optimistic on the reliability side of it. Herbivore-induced plant volatiles may not always be a 'short cut guide to dinner', and may in fact cause natural enemies to waste valuable time.

If I allowed for variation in the time wasted on non-hosts between parasitoid species, I always observed the 'wasteful' species going extinct first. As soon as the community was below an upper threshold of diversity, extinctions would stop. This resulted in communities of intermediate complexity. Parasitoids that wasted no time at all on non-hosts exhibited strong fluctuations, with minimum densities below one. Such perfect parasitoids would therefore go extinct as well. In this scenario the remaining communities contained only parasitoid species that waste relatively little time on non-hosts. From these results a picture emerges of on the one hand natural selection eliminating parasitoids that cannot deal with the complexity of the system, and on the other hand chance operating on small numbers eliminating parasitoids that are perfectly efficient (i.e. they are wasting no time on non-host herbivores).

The 'wasted time' mechanism has its greatest potential effect on the persistence of specialist natural enemies. This is in contrast with the mechanism proposed by McCann *et al.* (1998), in which weak trophic links dampen strong consumer-resource interactions. This mechanism works for generalists. McCann *et al.* (1998) predicted that specialist-dominated communities will be more variable than generalist-dominated ones. I predict that this will only hold if the 'wasted time' mechanism is not operating. This could be the case when plant information is specific, even under herbivory by a diverse assemblage of herbivores. In addition, natural enemies would have to be perfectly able to interpret this information. The persistence in my model system depends on the presence of several resource species. Each resource species contributes proportionally to persistence. This sheds a different light on the issue of redundancy (in the sense of having multiple species in a functional group, e.g. Naeem & Li 1997). Every single species may be important in determining community persistence. When studying the evolution of parasitoid-host interactions in the context of the diversity in natural food webs, more attention should be devoted to volatile production in natural plants infested with multiple herbivore species. Many of the modules in information webs are linked to plant infochemicals, especially in terrestrial food webs. Plant infochemicals have the potential to mediate a whole suite of trophic interactions, like parasitism or predation, intra-guild predation, exploitative competition between predators or parasitoids, apparent competition, and predation or parasitism by top carnivores or hyperparasitoids (see Dicke & Vet 1999; Vet 1999). It might well be interesting to investigate the relative effects of information web modules and food web modules on the stability of the entire system. My results show that a diverse community of herbivores and parasitoids can exist on one single plant species. I suggest that the 'wasted time' mechanism mediated by non-specific plant information, might well contribute to the brimming complexity we see in natural communities containing many more plant species than our single species example.

General conclusions

The parasitoid *C. glomerata* forages under incomplete information, in a complex environment. Its two main host species are difficult to locate. Solitarily feeding *P. rapae* larvae are inconspicuous, and clusters of the preferred host *P. brassicae* are rare. Information from the first trophic level in the form of herbivore-induced plant volatiles may be of little help, as a whole suite of nonhost herbivores may induce the production of highly similar plant volatile blends. Such odours from plants with nonhost herbivores are attractive to *C. glomerata* and cause these parasitoids to waste time. *C. glomerata*'s solution to this problem is a compromise. It leaves nonhost patches relatively quickly, exploits the less preferred *P. rapae* larvae that it encouters frequently and invests time in extensive explorative flights to locate rare *P. brassicae* clusters. The foraging strategy of *C. glomerata* combines a limited use of environmental cues with behavioural rules that work irrespective of the quality of environmental information. This may be the best it can do, given that herbivores are partly in control of the reliability of plant infochemicals.

Incomplete information is less problematic to *C. rubecula.* This parasitoid employs a simple and seemingly inflexible strategy, that is highly effective. *C. rubecula* do not need to invest time in explorative flights to locate a rare host. Interestingly, *C. glomerata* have lost a great deal of their tendency for explorative behaviour during a period of 350 generations in North America, where rare clustered hosts are absent. These parasitoids seem to minimise travel costs and effectively focus on the exploitation of *P. rapae.* My results suggest adaptive behavioural differentiation in *C. glomerata,* based on a loss of costly traits for dealing with a rare clustered host.

Incomplete information in parasitoids can result from defensive strategies in host and nonhost herbivores. The spatial distribution of nonhosts may be as important for the efficiency of parasitoid foraging strategies as the distribution of hosts. Nonhost herbivores, and their effect on the reliability of plant information should be included in evolutionary studies on parasitoid foraging behaviour.

Model results show that infochemical-mediated indirect effects of nonhost herbivores on specialist parasitoids may dramatically affect parasitoid community dynamics. Depending on herbivore diversity, such effects may either drive extinctions or promote the persistence of parasitoid communities.

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Samenvatting

Deze Nederlandse samenvatting heb ik geschreven voor niet-vakgenoten. Hij verschilt daarom van de Engelse samenvattende discussie, die meer gericht is op vakgenoten.

Sluipwespen zijn om verschillende redenen interessant en het bestuderen waard. Ze spelen een belangrijke rol binnen ecosystemen, vertonen een enorme soortenrijkdom en zijn van economisch belang door hun rol in de biologische bestrijding van plaaginsecten. Bovendien zijn het de modeldieren bij uitstek voor evolutionair ecologisch onderzoek. Sluipwespen worden ook wel parasitoïden genoemd. Vrouwelijke parasitoïden zoeken naar andere insecten om daar eitjes in te leggen. Een geparasiteerd insect dient als gastheer, een voedselbron voor de nakomelingen van de sluipwesp. De larven van veel soorten sluipwespen eten hun gastheer van binnenuit op. Als deze larven zich succesvol ontwikkelen, leidt dit tot de dood van de gastheer en het uitkomen van volwassen parasitoïden. Het aantal nakomelingen dat een sluipwesp kan krijgen, hangt nauw samen met de efficiëntie van haar zoekgedrag. Dit zoeken van sluipwespen naar gastheren wordt foerageren genoemd. Momenteel foerageren er tussen de 170.000 en 6 miljoen soorten sluipwespen op aarde. Daarmee nemen ze een belangrijke positie in: meer dan de helft van alle bekende diersoorten maakt deel uit van voedselwebben bestaande uit sluipwespen, herbivore insecten en planten. Als we meer inzicht krijgen in de werking van deze voedselwebben, kan dit een basis zijn voor dieper begrip van andere levensgemeenschappen, zowel op het land als in het water. Sluipwespen helpen mee met het groen houden van de wereld. Meer dan 216 biologische bestrijdingsprojecten in 99 landen hebben laten zien dat sluipwespen plaaginsecten volledig kunnen onderdrukken.

In dit onderzoek heb ik het foerageergedrag van sluipwespen onderzocht om evolutionaire en ecologische vragen te beantwoorden. De evolutionaire vragen, die ook wel functionele vragen worden genoemd, draaien om het waarom. Waarom foerageert een sluipwesp op deze manier en niet anders? Kunnen we dit gedrag begrijpen als een resultaat van natuurlijke selectie, een evolutionair proces? Leidt dit gedrag tot succes in het spel van overleving en voortplanting? De ecologische vragen richten zich meer op de werking van het systeem, de dynamiek en het voortbestaan van de interacties tussen sluipwespen, herbivoren en planten. Het kan zeer verhelderend zijn om verschillende typen vragen te combineren binnen één onderzoeksproject. Foerageerstrategieën lenen zich bij uitstek voor zo'n combinatie van ecologische en evolutionaire vragen. Deze strategieën bepalen voor een aanzienlijk deel de interactie-sterkte tussen sluipwespen, herbivoren en planten. Interactie-sterktes vormen het evolutionaire spanningsveld tussen bovengenoemde spelers en zijn de sleutel tot het begrijpen van voedselwebben.

Evolutie sinds Darwin

In 1883, het jaar nadat Darwin stierf, werd de sluipwesp *Cotesia glomerata* verscheept van Groot-Brittannië naar de Verenigde Staten. Aldaar werd *C. glomerata* losgelaten om koolwitjesrupsen te bestrijden in koolgewassen. De *Cotesia*'s vestigden zich al in 1884 en de opeenvolgende generaties sluipwespen hebben tot op de dag van vandaag naar gastheren gezocht in deze nieuwe omgeving. We kunnen nu zeggen dat met de introductie van *C. glomerata* in Noord Amerika onbedoeld een evolutionair veldexperiment werd ingezet. Europese en Noord Amerikaanse *C. glomerata* populaties hebben gedurende 350 generaties geleefd onder sterk verschillende ecologische omstandigheden.

Een belangrijk verschil tussen de twee omgevingen is de manier waarop gastheren verdeeld zijn over de ruimte. In Noord Amerika valt *C. glomerata* voornamelijk solitaire (alleen levende) larven van het kleine koolwitje (*Pieris rapae*) aan. Het grote koolwitje (*Pieris brassicae*), waarvan de larven in clusters van 7 tot 150 rupsen voorkomen, is afwezig in Noord Amerika. Deze twee koolwitjessoorten komen in Europa wel samen voor en worden hier beide aangevallen door de sluipwesp *C. glomerata*.

De foerageerstrategie van Europese *C. glomerata* sluipwespen is minder efficiënt bij het zoeken naar solitair voorkomende *P. rapae* rupsen dan de foerageerstrategie van de sluipwesp *Cotesia rubecula*, die gespecialiseerd is in het parasiteren van *P. rapae*.
Engelse onderzoekers hebben gevonden dat Amerikaanse *C. glomerata* sluipwespen nu efficiënter zijn in het aanvallen van *P. rapae* dan hun Britse soortgenoten. Dit suggereert dat *C. glomerata* zich heeft aangepast aan het parasiteren van deze gastheer in Noord Amerika. Uit het Engelse onderzoek werd echter nog niet duidelijk hoe het komt dat Amerikaanse sluipwespen tot een hogere aanvalssnelheid komen, omdat in het experiment geen gedragsobservaties werden gedaan.

Het hoofddoel van mijn onderzoek is het geven van een verklaring voor de variatie in zoekgedrag tussen verschillende populaties van *Cotesia* sluipwespen. Ik onderzoek of deze verschillen aanpassingen aan de omgeving kunnen zijn, wat de beperkingen zijn in de gedragsmogelijkheden

van de sluipwespen en welke mechanismes de dieren gebruiken om tot een bepaalde zoekstrategie te komen. Om aangeboren verschillen te bestuderen heb ik de zoekstrategieën van verschillende *Cotesia* populaties vergeleken in dezelfde omgeving. Om de effecten van variatie in de omgeving op zoekgedrag te bestuderen heb ik de voor de sluipwespen beschikbare informatie over de omgeving gevariëerd en jonge sluipwespen verschillende voorervaringen gegeven.
De proefopstellingen leken vaak op een veldsituatie, zodat de sluipwespen zoveel mogelijk hun natuurlijke gedragsrepertoire konden vertonen.

In het eerste deel van dit proefschrift beschrijf ik onderzoek aan de variatie in beslissingen van sluipwespen om gastheren te accepteren (om eitjes in te leggen) en in beslissingen om te vertrekken van de plekjes waarop die gastheren voorkomen. Beslissingen over gastheeracceptatie zijn belangrijk omdat de overlevingskans van sluipwespenlarven in verschillende soorten rupsen sterk kan verschillen. Vertrekbeslissingen zijn belangrijk omdat sluipwespen daarmee tijdverspilling kunnen voorkomen. Het heeft weinig zin om op een uitgeput plekje verder te zoeken als in de nabije omgeving veel betere plekjes met rupsen te vinden zijn. Sluipwespen hebben maar een beperkte levensduur en de parasitoïden die die tijd efficiënt gebruiken om naar gastheren te zoeken zullen relatief meer nakomelingen hebben.

In het tweede deel van dit proefschrift behandel ik variatie in het reisgedrag van *Cotesia glomerata*. De sluipwespen vliegen van blad tot blad, zowel binnen als tussen planten. Ze landen vaak op blaadjes met vraatschade en zoeken dan lopend verder naar rupsen. Er kan variatie zijn in reistijden tussen planten, in de relatieve hoeveelheid tijd die wordt besteed aan vliegend of lopend zoeken en in de neiging om binnen dezelfde plant verder te zoeken of juist naar een andere plant te vliegen als de sluipwesp van een blaadje vertrekt. Al deze aspecten bepalen hoe efficiënt een bepaalde foerageerstrategie is bij een bepaalde ruimtelijke verdeling van gastheren. Bij dit onderzoek heb ik gebruik gemaakt van gedragsobservaties en een gedetailleerd simulatie-model. Ik gebruikte de simulaties om te onderzoeken hoe alternatieve foerageerstrategieën leiden tot verschillen in reproductief succes ('t behaalde aantal nakomelingen), in omgevingen met verschillende ruimtelijke verdelingen van gastheren.

Voor het derde deel van dit proefschrift heb ik gebruik gemaakt van experimentele resultaten, veldgegevens en een eenvoudig model, om te onderzoeken hoe het sluipwespengedrag doorwerkt op de dynamiek van de levensgemeenschap van sluipwespen en herbivoren op koolplanten.

Hierbij schalen we dus op van onze kennis van individuele dieren, naar de schommelingen in aantallen dieren in de loop van de tijd. Ik zal hieronder de belangrijkste doelstellingen van dit onderzoek noemen, mijn resultaten samenvatten en dit stuk afsluiten met mijn algemene conclusies.

De drie belangrijkste doelstellingen van dit onderzoek waren het evalueren en begrijpen van 1) verschillen tussen *C. glomerata* en *C. rubecula* in het gebruiken van informatie tijdens de exploitatie van plekjes met gastheren, 2) het belang van gedragsverschillen tussen Europese en Noord Amerikaanse *C. glomerata* populaties voor het behalen van reproductief succes en 3) de effecten van een beperkt informatiegebruik door sluipwespen op het functioneren van de levensgemeenschap van sluipwespen en herbivoren op koolplanten.

Interspecifieke variatie (verschillen tussen sluipwespensoorten)

In Europa accepteren zowel *C. glomerata* als *C. rubecula* het kleine koolwitje, *P. rapae* als gastheer. *C. rubecula* is een specialist op *P. rapae*, terwijl *C. glomerata* een voorkeur heeft voor *P. brassicae*. Deze voorkeuren weerspiegelen hoe geschikt de verschillende gastheren zijn voor de ontwikkeling van *Cotesia glomerata* en *C. rubecula*. De larven van *P. rapae* en *P. brassicae* verschillen in hun ruimtelijke verdeling op planten. *P. rapae* larven eten solitair van bladeren en volgen vaak een Poisson verdeling over planten. Daarbij is zowel het aantal rupsen op een plant als de spreiding in het aantal rupsen op een plant erg laag. Op ongeveer 1 op de 10 koolplanten zit *P. rapae*. Op zo'n besmette plant zitten meestal maar 1 of 2 rupsen. De larven van *P. brassicae* eten in een groep van een blad en komen op planten in zeer variabele aantallen van 7 tot 150 rupsen voor. Deze *P. brassicae* clusters zijn in de meeste jaren zeldzaam in Europa. Meestal is er slechts 1 cluster te vinden in een groep van 250 koolplanten. In sommige jaren kan *P. brassicae* echter massaal voorkomen.

Onervaren *C. rubecula* and *C. glomerata* sluipwespen worden aangetrokken door planten met *Pieris*-schade. Het maakt hierbij niet uit of deze schade door het grote of het kleine koolwitje is veroorzaakt. Daardoor zullen beide soorten *Cotesia* in Europa foerageren op verschillende typen blaadjes, zowel met gastheren waar ze voorkeur voor hebben als met gastheren die ze niet prefereren. Dit leidt tot de vraag hoe beide *Cotesia*-soorten zullen omgaan met de verschillende typen door *Pieris* aangevreten bladeren, en welke informatie en ervaringen ze gebruiken om exploitatie-beslissingen te nemen op deze bladeren.

In **hoofdstuk 2** heb ik gebruik gemaakt van een statistisch model (Cox' proportional hazards model) om de vertrekneigingen te analyseren van *C. rubecula* en *C. glomerata*. De vertrekneiging is de kans per seconde om van een blaadje weg te vliegen. De sluipwespen foerageerden in een omgeving met geprefereerde gastheren, niet geprefereerde gastheren, of een combinatie van die twee. *C. rubecula* gebruikte een eenvoudige strategie. De vertrekneiging was hoog op bladeren die leeg waren, of aangevreten door de niet geprefereerde gastheer, vooral in de omgeving waar alleen *P. brassicae* aanwezig was. Dit zal er toe leiden dat *C. rubecula* weinig tijd besteedt aan onvoordelige plekjes en meer tijd zal investeren op blaadjes met *P. rapae*. De sluipwesp *C. rubecula* leek geen gebruik te maken van voorafgaande ervaringen om vertrekbeslissingen te nemen op het huidige blad. Het valt ook niet te verwachten dat leergedrag het foerageersucces kan verbeteren in een omgeving waarin geïnfecteerde planten willekeurig zijn verdeeld over de ruimte en waarin gastheren meestal in hun eentje op een blad voorkomen.

C. glomerata vertoonde veel flexibeler gedrag tijdens het foerageren in een omgeving met de geclusterde gastheer. Ontmoetingen met gastheren beïnvloedden de vertrekneiging op het huidige plekje. Dit effect werkte nog door tijdens latere plekbezoeken aan andere bladeren. De vertrekneiging van blaadjes veranderde ook naarmate het aantal bezoeken aan verschillende aangevreten blaadjes toenam. *C. glomerata* vertoonde echter net zulk eenvoudig gedrag als *C. rubecula* in de omgevingen waar alleen *P. rapae* of beide gastheren aanwezig waren. Dit suggereert dat *C. glomerata* zijn flexibelere foerageergedrag misschien alleen gebruikt in de jaren dat er buitengewoon hoge aantallen van *P. brassicae* voorkomen. Eén aspect aan het vertrekgedrag van *C. rubecula* and *C. glomerata* was verrassend. De sluipwespen vertrokken niet meteen na een ovipositie in *P. rapae*, zelfs als er maar één larve op het plekje aanwezig was. Dit is tijdverspilling. Verder leek geen van beide *Cotesia* soorten gebruik te maken van chemische informatie over het aantal gastheren op een blad, om hun vertrekneiging af te stemmen. De sluipwespen hadden alleen verschillende vertrekneigingen op schone en aangevreten blaadjes. Zo'n verspilling van tijd en een beperkt gebruik van informatie lijken een gebrek aan aanpassing aan de huidige verdeling van Europese *P. rapae* larven over blaadjes te weerspiegelen. Daarbij dient wel te worden vermeld dat de concentratie van infochemicaliën (geurstoffen) een onbetrouwbare bron van informatie kan zijn, bij voorbeeld omdat predatoren regelmatig rupsen van blaadjes verwijderen. Een strategie die onbetrouwbare informatie gebruikt voor het inschatten van het aantal gastheren op plekjes zal het reproductief succes niet verhogen.

We kunnen ons ook afvragen wat voor rupsen de beste strategie is om over de ruimte verdeeld te zijn bij een bepaalde zoekstrategie van de sluipwespen. Gegeven dat de sluipwespen slechts beperkt gebruik maken van informatie en gegeven dat ze langer blijven op een plekje na elke parasitering, is het solitair voorkomen op plekjes waarschijnlijk het beste wat *P. rapae* kan doen. Dit zal het risico op parasitering van individuele rupsen minimaliseren, omdat het een maximale tijdverspilling bij de sluipwespen veroorzaakt. Ondanks de genoemde beperkingen is de specialist *C. rubecula* toch vrij efficiënt in het foerageren op *P. rapae*, zeker in vergelijking met *C. glomerata*. De sluipwesp *C. rubecula* heeft een korte tijd nodig om een *P. rapae* larve te vinden op een blad en kan daardoor ook een hogere vertrekneiging op bladeren hebben. Op deze manier lijkt deze sluipwesp haar tijdverspilling te minimaliseren. *C. glomerata* heeft meer tijd nodig om *P. rapae* op een plekje te vinden. Daarom moeten deze sluipwespen een relatief lage vertrekneiging hebben om toch kans te maken op het ontmoeten van een gastheer, voordat het plekje wordt verlaten.

C. glomerata is zeer efficiënt in het foerageren op plekjes met *P. brassicae*. Het probleem zit meer in het localiseren van de zeldzame *P. brassicae* clusters. De overvloed aan plekjes met *P. rapae* maskeert tot op zekere hoogte de aanwezigheid van *P. brassicae* clusters. Deze clusters zouden veel meer opvallen als er geen andere herbivoren (planteneters) op koolplanten zaten. Dan zouden namelijk alleen de met *P. brassicae* geïnfecteerde planten naar vraatschade ruiken. *Cotesia* sluipwespen en *Pieris* gastheren zijn verwikkeld in een dynamisch spel van zoeken en verstoppen waarbij de kosten en baten van verschillende strategieën blijven veranderen terwijl de spelers hun nieuwe zetten doen in de loop van de evolutie. Sluipwespen en gastheren kunnen chemische informatie gebruiken, zowel bij aanval als bij verdediging. Daarbij is het mogelijk dat ze inspelen op beperkingen in de zintuigfysiologie en het informatiegebruik van hun tegenspelers.

Een vergelijking van Europese en Noord Amerikaanse *C. glomerata* populaties

De drie belangrijkste verschillen tussen Europa (Groot Brittannië inbegrepen) en de Verenigde Staten zijn dat 1) de geclusterde en meest geschikte gastheer *P. brassicae* afwezig is in Noord Amerika, 2) *P. rapae* hoge dichtheden bereikt gedurende de zomer in Noord Amerika, terwijl *P. rapae* dichtheden veel lager blijven in Europa. Bij die hogere aantallen rupsen hoort een ruimtelijke verdeling (negatief binomiaal) waarbij de spreiding in het aantal rupesen op planten relatief groter is dan bij de al genoemde Poisson verdeling. 3) *C. rubecula* afwezig is in de meeste staten van de USA.

Deze verandering in belangrijke aspecten van de leefomgeving voor de geïntroduceerde *C. glomerata* populatie roept verschillende vragen op. Accepteren Amerikaanse *C. glomerata* sluipwespen nog steeds *P. brassicae*, terwijl er al 350 generaties geen contact is geweest met deze gastheer? Gebruiken Amerikaanse *C. glomerata* sluipwespen ruimtelijk foerageergedrag dat efficiënter is bij het zoeken naar *P. rapae* dan dat van Europese *C. glomerata*'s? Welke gedragsmechanismen liggen ten grondslag aan zulke variatie? In de hoofdstukken drie, vier en vijf beschrijf ik mijn onderzoek aan gedragsverschillen tussen Europese and Noord Amerikaanse *C. glomerata* populaties.

In **hoofdstuk 3** behandel ik variatie in gastheeracceptatie. *Cotesia* sluipwespen van verschillende populaties zijn vergeleken in hun gastheeracceptatiegedrag nadat deze hun ontwikkeling hadden doorgemaakt in dezelfde soort gastheer. Fenotypische verschillen (omgevingseffecten) werden onderzocht door de sluipwespen hun ontwikkeling in verschillende soorten gastheren door te laten maken.

Als Europese en Amerikaanse parasitoïden zowel gekweekt als getest werden op *P. rapae*, dan was er geen genotypisch verschil in acceptatie van *P. rapae* als gastheer tussen deze stammen. Als daarentegen beide sluipwespenlijnen werden gekweekt op *P. rapae*, maar getest op *P. brassicae*, dan accepteerden de Amerikaanse parasitoïden significant minder vaak *P. brassicae* dan hun Europese soortgenoten. De Amerikaanse dieren lijken een aanzienlijk deel van hun neiging om deze gastheer te parasiteren verloren te hebben gedurende de honderden generaties dat deze gastheer niet beschikbaar was in Noord Amerika. Europese *C. glomerata*'s keurden *P. rapae* significant vaker af na ontwikkeling in *P. brassicae* dan wanneer *P. rapae* de gastheer was geweest waarin ze zich ontwikkelden. Sluipwespen kunnen als ze uit hun kokon komen daarop infochemicaliën ruiken die van hun gastheer afkomstig zijn. Deze informatie kunnen ze benutten als een aanwijzing dat *P. brassicae* aanwezig is in de omgeving en vervolgens gebruiken om de minder geschikte *P. rapae* larven af te keuren. De meeste Europese *C. glomerata*'s accepteerden onmiddelijk *P. brassicae* als gastheer, ongeacht of ze zich in *P. rapae* of *P. brassicae* ontwikkeld hadden. Dit komt overeen met het idee dat *P. brassicae* de geprefeerde en meest geschikte gastheer van *C. glomerata* is in Europa.

Daarnaast heb ik onderzocht of de ervaring van het leggen van eieren in de voorkeursgastheer *P. brassicae* zou leiden tot het afkeuren van daarna aangeboden *P. rapae* larven, door Europese *C.*

glomerata's. In tegenstelling tot wat ik in eerste instantie verwachtte, veranderde de acceptatie van de minder geschikte *P. rapae* larven niet na ovipositie-ervaringen met de meer geschikte *P. brassicae* larven. Toch valt dit resultaat goed te begrijpen. Om een serie oviposities te gebruiken als een aanwijzing voor de aanwezigheid van *P. brassicae* in de omgeving is wel erg 'mosterd na de maaltijd'. Als een *C. glomerata* sluipwesp een cluster van *P. brassicae* vindt, kan ze waarschijnlijk al haar eieren in deze gastheren leggen. Daarna is het niet meer relevant of *P. rapae* afgekeurd zou moet worden. Daarom zijn oviposities in *P. brassicae* waarschijnlijk geen nuttige bron van informatie voor sluipwespen die moeten beslissen of ze de *P. rapae* larven die ze vaker tegen komen wel of niet zullen accepteren.

In de Verenigde Staten is er vele generaties lang geen voordeel geweest om specifieke informatie te gebruiken die aan *P. brassicae* gerelateerd is tijdens het zoeken naar gastheren. Er is ook geen selectiedruk geweest op het behouden van een hoog acceptatie-niveau van *P. brassicae*, of om gedrag in stand te houden dat efficiënt is bij de exploitatie van plekjes met geclusterde gastheren.

Van verschillende sluipwespenssoorten is bekend dat ervaring wel de gastheer-acceptatie van minder geprefereerde gastheren verandert, maar niet van geprefereerde gastheren. Dit effect op de acceptatie van minder geprefereerde gastheren kwam ook voor in het *Cotesia-Pieris* systeem: ervaring als gevolg van ontwikkeling in een bepaalde gastheer beïnvloedde wel de acceptatie van *P. rapae* larvae, maar niet van de geprefereerde gastheer *P. brassicae*. Kennelijk zit de acceptatie van een gastheer van hoge kwaliteit tot op zekere hoogte 'ingebakken' in deze sluipwespen, terwijl de acceptatie van gastheren van lagere kwaliteit veel flexibeler is, zodat daarop kan worden teruggevallen in omstandigheden waarin de beste gastheer niet beschikbaar is.
Het is interessant dat de 'ingebakken' hoge acceptatie van *P. brassicae* verloren lijkt te zijn gegaan gedurende de 350 generaties dat *C. glomerata* geen toegang had tot deze gastheer in Noord Amerika. Ook bij andere diersoorten, bij voorbeeld bij stekelbaarsjes, treedt gedragsdifferentiatie tussen geografisch gescheiden populaties vaak op door het verlies van (delen van) gedragspatronen. Een ander aspect van *C. glomerata*-gedrag dat gedifferentieerd zou kunnen zijn is het reisgedrag, omdat in Europa uitgebreide vluchten nodig zijn om zeldzame clusters van *P. brassicae* te localiseren en in Noord Amerika niet.

In **hoofdstuk 4** beschrijf ik het reisgedrag van *C. glomerata*'s van Europese en Noord Amerikaanse stammen in een omgeving met verscheidene planten, die een veldsituatie nabootst.

Sluipwespen van de Europese stam cirkelden boven meer planten, hadden meer en langere reistijden tussen planten, hadden een hogere proportie vluchten tussen planten en bezochten meer blaadjes met gastheren dan de Noord Amerikaanse *C. glomerata*'s in dezelfde omgeving. De Europese sluipwespen kwamen op veel blaadjes en doorzochten die voor een relatief korte tijd, terwijl de Amerikaanse sluipwespen slechts op enkele blaadjes kwamen, maar die wel langdurig en grondig doorzochten. Amerikaanse *C. glomerata*'s hadden meer oviposities per plekbezoek dan de Europese *C. glomerata*'s. Deze verschillen in ruimtelijk foerageergedrag duiden op een meer exploratieve (verkennende) strategie bij de Europese *Cotesia*'s, en op een meer op exploitatie gerichte strategie bij de Noord Amerikaanse *Cotesia*'s. Mijn hypothese is dat het uitgebreide rondvliegen tussen planten bij Europese *C. glomerata*'s een mechanisme is om *P. brassicae* te localiseren. In Noord Amerika zijn exploratieve vluchten waarschijnlijk minder nuttig, omdat vliegen energetisch erg kostbaar is, terwijl de opbrengst, namelijk het vinden van zeldzame gastheren van hoge kwaliteit, afwezig is in deze omgeving.

Sluipwespen gebruiken informatie uit hun directe omgeving, maar de precieze omvang van deze 'directe omgeving' is vaak onbekend. In een volgend experiment onderzocht ik of de sluipwespen olfactorische informatie (geuren) van een nabij gelegen plekje gebruikten terwijl ze foerageerbeslissingen nemen op het huidige plekje. Ik heb laten zien dat er geen meetbaar effect was van een nabij gelegen plek met een cluster van de voorkeurs-gastheer *P. brassicae* op de vertrekneiging van *C. glomerata* sluipwespen. Dit is verrassend, omdat het toch zeer voordelig zou zijn om snel een slecht plekje te verlaten als een een zeer goed plekje 60 cm verderop aanwezig is. Tijdens voorbereidende experimenten merkte ik al dat de respons van *C. glomerata* op een aangevreten blad het sterkst was op een afstand van 0 tot 30 centimeter. Dit is ook de afstand die sluipwespen aanhouden als ze boven blaadjes rondcirkelen. Deze resultaten geven aan dat het uitgebreide vliegen tussen planten en cirkelen boven planten essentiëel kan zijn voor het vinden van zelfs een zeer nabijgelegen cluster *P. brassicae* larven. Dit cirkelen tussen en boven planten leek het sterkst aanwezig te zijn bij Europese *C. glomerata*'s die zich ontwikkeld hadden in *P. brassicae*. Dit suggereert dat *C. glomerata* vroege ervaringen met *P. brassicae* gebruikt als aanwijzing dat deze voorkeurs-gastheer in de omgeving aanwezig is, en haar zoekgedrag daarop afstemt.

De boven-genoemde resultaten geven aan dat foerageerbeslissingen voornamelijk worden genomen op basis van informatie uit de directe omgeving, en dat *C. glomerata* sluipwespen niet gelijktijdig olfactorische informatie van verschillende nabijgelegen plekjes gebruiken bij het nemen van beslissingen op het huidige plekje. Hier staat tegenover dat *C. glomerata* sluipwespen zeer regelmatig terugkwamen op al bezochte plekjes, na bezoeken op andere plekjes. Dit kan in principe informatie-gebruik op een wijdere ruimtelijke schaal mogelijk maken. Alhoewel het niet meteen duidelijk is wat het voordeel is van zulke herbezoeken, zijn deze resultaten toch belangrijk vanuit theoretisch oogpunt: Beslissingen die in eerste instantie op een blaadje worden genomen hoeven niet de eindbeslissing van een sluipwesp met betrekking tot dat plekje te vertegenwoordigen. De exploitatie van plekjes kan worden geregeld door een meertraps beslissingsproces, waarbij beslissingen worden bijgesteld nadat de sluipwesp ervaring heeft opgedaan op verschillende andere plekjes in de omgeving.

In **hoofdstuk 5** beschrijf ik hoe de verschillen in foerageergedrag tussen Amerikaanse en Europese *Cotesia*'s zich vertalen in het aantal nakomelingen dat zij krijgen gedurende hun hele leven, wat ik hierna reproductief succes zal noemen. Met een gedetailleerd simulatie-model extrapoleerde ik van mijn experimentele resultaten naar het foerageergedrag gedurende een heel sluipwespenleven in omgevingen met verschillende ruimtelijke verdelingen van *P. rapae*. De zoekstrategie van Amerikaanse *Cotesia*'s resulteerde in een hoger reproductief succes op een Poisson verdeling van *P. rapae*. Zo'n verdeling komt normaal gesproken voor in Europa en vroeg en laat in het seizoen in Noord Amerika. Het reproductieve succes van de verschillende stammen verschilde niet op de negatief binomiale verdeling, die karakteristiek is voor midzomerse *P. rapae* populaties in Noord Amerika. De 'Europese strategie' betaalde voor de lange exploratieve vluchten tussen planten, terwijl dat nooit kon resulteren in het vinden van een *P. brassicae* cluster. In de omgeving was immers alleen *P. rapae* aanwezig. De 'Amerikaanse strategie' verspilde geen tijd aan zulke vluchten en investeerde veel tijd aan het op plekjes zoeken naar *P. rapae*. Het reproductieve succes als gevolg van de Europese foerageerstrategie was het meest gevoelig voor een toename in de opgeeftijd op blaadjes. Juist hierin verschilden de Amerikaanse sluipwespen het meest van hun Europese soortgenoten. De Noord Amerikaanse *C. glomerata*'s hadden een 121 procent hogere opgeeftijd op blaadjes.

In de eerste simulaties waren de sluipwespen niet in staat van een afstand onderscheid te maken tussen verschillende gastheerdichtheden op geïnfecteerde planten en bladeren. In daarop volgende simulaties stonden we de sluipwespen toe om informatie over de hoeveelheid vraatschade op planten en/of bladeren waar te nemen in hun nabije omgeving, en om deze informatie te benutten door bij voorkeur te landen op plekjes met veel gastheren. Het reproductieve succes van de *C. glomerata*'s nam niet significant toe bij zo'n verhoogde waarneming van vraatschadeniveaus en het gebruik van deze informatie. Dit komt waarschijnlijk doordat de huidige vertrekstrategie niet is afgestemd op het efficiënt gebruiken van deze informatie over gastheerdichtheden.

In Europa zit op minder dan 1 op de 20 door *Pieris* geïnfecteerde planten een cluster van *P. brassicae*. In de simulaties bezocht slechts tien procent van de Europese sluipwespen meer dan twintig planten met *Pieris*-schade. Dit geeft aan dat de kans van een Europees *C. glomerata* vrouwtje om tijdens haar leven een *P. brassicae* cluster tegen te komen laag is, bij de huidige strategie voor reizen en exploiteren van plekjes.

De simulaties lieten zien dat het reproductieve succes van Noord Amerikaanse *C. glomerata*'s lager zou zijn in een omgeving waar *P. rapae* vlinders altijd een enkel eitje op een schoon blad zouden leggen. Bij de ruimtelijke verdeling van *P. rapae* die daaruit zou voortvloeien, zou het risico van parasitering voor individuele larven lager zijn. Waarschijnlijk leggen *P. rapae* vlinders inderdaad het liefst enkele eitjes op schone bladeren. De vliegkunst van koolwitjes kent echter zijn beperkingen en onder winderige omstandigheden zal slechts een beperkt aantal koolblaadjes geschikt zijn om op te landen. Dit kan resulteren in de hogere dichtheden per blad bij midzomerpopulaties van Noord Amerikaanse kleine koolwitjes.

De variatie in foerageergedrag tussen Amerikaanse en Europese *C. glomerata*'s is meer dan een kleine verandering in een enkel kenmerk. Alle gedragsparameters voor de aankomstkansen op plekjes, vertrekneigingen en reistijdbeslissingen varieërden aanzienlijk tussen deze populaties. De waardes hiervoor van de Amerikaanse sluipwespen waren van zo'n 66 procent lager tot 121 procent hoger dan die van hun Europese soortgenoten. Het gedrag van deze sluipwespen ligt in opmerkelijk verschillende gebieden in de parameterruimte.

Incomplete informatie: consequenties voor de levensgemeenschap

In **hoofdstuk 6** I laat ik zien hoe de aanwezigheid van andere soorten herbivoren, die geen gastheer zijn, het foerageergedrag van *C. glomerata* beïnvloedt. Op basis van deze resultaten heb ik een model gemaakt om de potentiële effecten op het niveau van de levensgemeenschap te onderzoeken. *C. glomerata* gebruikt door herbivoren geïnduceerde vluchtige plantenstoffen om gastheren te localiseren. Omdat planten meestal door een complex van herbivoren worden aangevallen, vroeg ik me af hoe sluipwespen omgaan met chemische planteninformatie die het gevolg is van vraat door zowel gastheren als andere herbivoren.

De experimentele resultaten lieten zien dat *C. glomerata* in de problemen komt als ook andere herbivoren schade aan de planten veroorzaken. De sluipwespen werden aangetrokken door infochemicaliën van blaadjes met andere soorten herbivoren en besteedden een aanzienlijke hoeveelheid tijd aan zulke blaadjes. Wanneer plantengeuren niet duidelijk aangeven welke soorten herbivoren op een bepaald moment schade veroorzaken, dan zal een toename in de diversiteit van herbivoren de interactie-sterktes tussen gastheren en specialistische sluipwespen verzwakken. Uit de modelresultaten blijkt dat het voortbestaan (de persistentie) van gemeenschappen van sluipwespen en herbivoren wordt bevorderd door een toename in diversiteit als die gaat van zeer weinig soorten naar een meer diverse gemeenschap. Er is echter een drempelwaarde van diversiteit waarboven de sluipwespen kunnen uitsterven doordat ze te veel worden gehinderd door de aanwezigheid van herbivoren die geen gastheer zijn.

Zo kan diversiteit het voortbestaan van populaties bevorderen, maar ook leiden tot het uitsterven van die populaties, als diversiteit tijdverspilling veroorzaakt bij sluipwespen.

'Tijdverspilling' is waarschijnlijk een zeer algemeen fenomeen in de ecologie van dieren, met als andere voorbeelden wederzijdse interferentie (hindering) tussen predatoren, het aangetrokken worden van sluipwespen door planten waarop nooit gastheren zitten, en prooien die in een refugium (schuilplaats) blijven waar ze niet kunnen eten.

Verschillende soorten herbivoren die samen voorkomen op een enkele plantensoort zijn misschien concurrenten in termen van het voedselweb, maar werken samen via het 'informatie-web'. Als een complex van herbivoren plantengeuren minder informatief maakt, dan zal elke herbivoor in dat complex iets meer beschermd zijn tegen specialistische natuurlijke vijanden en, in mindere mate ook tegen generalisten. Mijn experimenten tonen duidelijk aan dat de sluipwespen geen enkel probleem hebben om blaadjes te vinden met gastheren, als er geen andere herbivoren aanwezig zijn. Echter, dit vermogen neemt significant af in de aanwezigheid van andere planteneters. Het grootste deel van de literatuur over vluchtige stoffen van door herbivoren beschadigde planten neemt aan dat deze geuren, ook wel synomonen genoemd, natuurlijke vijanden naar de herbivoren leiden. Daarmee zouden planten een belangrijk foerageerprobleem oplossen door natuurlijke vijanden van betrouwbare en goed waarneembare chemische informatie over herbivoren te voorzien. Mijn onderzoek laat zien dat dit gezichtspunt ten minste voor spruitkoolplanten te optimistisch is wat betreft de betrouwbaarheid van synomonen. Door herbivoren geïnduceerde vluchtige plantenstoffen kunnen de olfactorische variant op een dwaallicht zijn, en de oorzaak van aanzienlijke tijdverspilling bij natuurlijke vijanden.

Als ik in het model variatie toeliet in de tijd die verschillende soorten sluipwespen besteden aan andere herbivoren, dan zag ik altijd dat de meest 'spilzieke' sluipwespen als eerste uitstierven. Zodra de gemeenschap onder een bepaalde kritische soortenrijkdom kwam, traden geen extincties meer op. Dit resulteerde in gemeenschappen die niet sterk verarmd, maar ook niet erg complex waren. Sluipwespen die in het geheel geen tijd verspilden aan andere herbivoren vertoonden sterke fluctuaties in aantallen, met zeer lage minimum dichtheden. Deze sluipwespen zijn zo efficiënt, dat ze hun gastheren regelmatig tot op de grens van uitsterven brengen, waardoor hun eigen populatie ook regelmatig bijna ten onder gaat. Zulke 'perfecte' sluipwespen zouden daardoor in de praktijk ook een groot risico op uitsterven hebben. In dit scenario bevatten de overgebleven levensgemeenschappen alleen sluipwespensoorten die relatief weinig tijd verspillen aan herbivoren die geen gastheren zijn. Uit deze resultaten komt een beeld naar voren van natuurlijke selectie aan de ene kant, die juist die sluipwespen elimineert die niet weten om te gaan met de complexiteit van het systeem, en aan de andere kant het toeval, dat inwerkt op zeer lage minimum populatie-aantallen, dat de sluipwespen elimineert die op het perfecte af efficiënt zijn (omdat ze geen tijd verspillen aan andere soorten herbivoren).

Het 'verspilde tijd' mechanisme heeft potentiëel het grootste effect op het voortbestaan van specialistische natuurlijke vijanden. Dit in tegenstelling tot een mechanisme dat wel het 'zwakke interactie' effect wordt genoemd. Daarbij kunnen zwakke interacties tussen sommige natuurlijke vijanden en prooien de sterke interacties dempen tussen andere predatoren en prooien. Dit zwakke interactie effect werkt alleen bij generalisten en leidt tot de voorspelling dat door specialisten gedomineerde levensgemeenschappen sterkere fluctuaties zullen vertonen dan de levensgemeenschappen die door generalisten worden gedomineerd. Ik voorspel dat dit alleen zo kan zijn als het 'verspilde tijd' mechanisme in een bepaald systeem niet belangrijk is. Dat zou zo kunnen zijn wanneer plantengeuren specifieke betrouwbare informatie geven, zelfs als er een complex van herbivoren aanwezig is. Daarnaast zouden natuurlijke vijanden dan ook nog in staat moeten zijn om deze informatie correct te interpreteren. Het voortbestaan van de soorten in mijn model systeem hangt af van de aanwezigheid van verschillende gastheersoorten. Elke gastheersoort draagt proportioneel bij aan het voortbestaan van het systeem. Dit werpt een nieuw licht op het idee van 'redundantie' (in de zin van het voorkomen van meer soorten binnen een functionele groep van organismen, zoals planten of herbivoren). Het is mogelijk dat elke soort een belangrijke bijdrage levert aan het voortbestaan van de levensgemeenschap. Bij onderzoek aan de evolutie van sluipwesp-gastheer interacties, in de context van diversiteit in natuurlijke voedselwebben, zou meer aandacht mogen worden besteed aan de productie van vluchtige plantenstoffen in wilde planten die geïnfecteerd zijn met verschillende soorten herbivoren. Veel van de modules (subsystemen) in informatiewebben zijn verbonden met infochemicaliën van planten, in het bijzonder in terrestrische voedselwebben. Zulke synomonen kunnen als middelaar optreden bij een scala aan (trofische) interacties, zoals parasitisme of predatie, 'intra-guild predation', exploitatieve concurrentie tussen predatoren of sluipwespen, 'apparent competition', en predatie of parasitering door topcarnivoren of hyper-parasitoïden (sluipwespen van sluipwespen). Het zou interessant zijn om te onderzoeken wat de relatieve effecten zijn van informatieweb-modules en voedselweb-modules op de stabiliteit van het hele systeem. Mijn modelresultaten laten zien dat een diverse levensgemeenschap van herbivoren en sluipwespen kan voortbestaan op een enkele plantensoort. Deze resultaten suggereren dat het 'verspilde tijd' mechanisme, dat wordt veroorzaakt door niet-specifieke planten-informatie een steentje bijdraagt aan de overweldigende complexiteit die we zien in natuurlijke levensgemeenschappen, die veel meer plantensoorten bevatten dan ons voorbeeld-systeem.

Algemene conclusies

De parasitoïde *C. glomerata* foerageert in een complexe leefomgeving, terwijl daarover slechts beperkte informatie beschikbaar is. De twee belangrijkste gastheren zijn moeilijk te vinden. Solitaire *P. rapae* rupsen zijn onopvallend, en clusters van de geprefereerde gastheer *P. brassicae* zijn zeldzaam. Informatie van het eerste trofische niveau in de vorm van door vraat-geïnduceerde plantengeuren is maar van beperkte waarde, omdat een scala aan herbivoren die geen gastheer zijn de productie van vrijwel dezelfde plantengeuren induceren. Zulke geuren van planten met schade, maar zonder gastheren zijn aantrekkelijk voor *C. glomerata* en veroorzaken dat de sluipwespen tijd verspillen. *C. glomerata*'s oplossing voor dit probleem is een compromis. De sluipwespen bezoeken weliswaar plekjes waarop andere herbivoren zitten, maar ze blijven daar relatief kort. *C. glomerata* exploiteert de larven van *P. rapae*, waarvoor ze geen voorkeur heeft, maar die ze wel regelmatig tegen komt en investeert tijd in uitgebreide exploratieve vluchten om zeldzame *P. brassicae* clusters te localiseren. De foerageerstrategie van *C. glomerata* combineert een beperkt gebruik van prikkels uit de omgeving met gedragsregels die werken, ongeacht de kwaliteit van de informatie uit de omgeving. Dit zou heel goed het best haalbare kunnen zijn, gegeven dat herbivoren gedeeltelijk bepalen hoe (on-)betrouwbaar de geur-informatie van aangevreten planten is.

Incomplete informatie is minder problematisch voor *C. rubecula*. Deze sluipwesp past een simpele en schijnbaar inflexible strategie toe, die zeer effectief is. *C. rubecula* hoeft geen tijd te investeren in exploratieve vluchten om een zeldzame geclusterde gastheer te vinden. Interessant genoeg heeft *C. glomerata* een groot deel van deze neiging tot exploratief gedrag verloren gedurende een periode van 350 generaties in Noord Amerika, waar zeldzame geclusterde gastheren niet voorkomen. Deze sluipwespen lijken reiskosten te minimaliseren en zich effectief te richten op het exploiteren van *P. rapae*. Mijn resultaten suggereren adaptieve gedragsdifferentiatie in *C. glomerata*, gebaseerd op een verlies van 'dure' eigenschappen voor het gebruiken van een zeldzame geclusterde gastheer.

Incomplete informatie in sluipwespen kan het gevolg zijn van defensieve strategieën van herbivoren. Deze kunnen gezamenlijk voorkomen op planten, en daardoor de informatievoorziening aan sluipwespen van die planten bemoeilijken. Daarmee wordt de ruimtelijke verdeling van herbivoren die geen gastheer zijn net zo belangrijk voor de efficiëntie van een bepaalde sluipwesp als de verdeling van gastheren. Herbivoren die geen gastheer zijn, en hun effect op de betrouwbaarheid van planteninformatie zouden meegenomen moeten worden in evolutionaire studies naar het foerageergedrag van parasitoïden.

Model-resultaten laten zien dat herbivoren die geen gastheer zijn, via planten-infochemicaliën belangrijke indirecte effecten kunnen hebben op de dynamiek van levensgemeenschappen van sluipwespen en herbivoren. Afhankelijk van de diversiteit aan herbivoren, kunnen zulke effecten het plaatselijk uitsterven van sluipwespensoorten veroorzaken, of juist het voortbestaan van levensgemeenschappen bevorderen.

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Matthijs,
Nieuwersluis, 22 april 2001

Curriculum Vitae

My name is Matthijs Vos. I was born in Enschede, The Netherlands, on the sixth of June 1971. I completed my secondary education (V.W.O.) at Erasmus College in Zoetermeer, in 1990. I started to study biology at Leiden University in the same year.

In 1993 I studied sex ratios and the mating structure of a parasitoid that attacks citrus mealybugs, during an 8-month research project for my MSc. This research was performed at the Leiden Animal Ecology Department, under supervision of Jacques van Alphen, in collaboration with Entocare, a biological control company. For another 8-month research project I spent 4 months at the International Institute of Tropical Agriculture (IITA) in Benin, Afrika, to study host stage selection and sex allocation in two parasitoids of the mango mealybug. The remaining 4 months were used to develop a stage structured model for the population dynamics of this pest insect and its parasitoids. This project was supervised by Peter Neuenschwander at IITA and by Jacques van Alphen in Leiden.

I received my Master's degree, cum laude, from Leiden University in January 1995 and started my PhD work at Wageningen University in February 1995. My project was a collaboration between the Laboratory for Entomology and the Subdepartment of Mathematics. This research on the *Adaptation of parasitoid foraging strategies to the spatial distribution of host species* was supervised by Louise Vet and Lia Hemerik, and under the aegis of Joop van Lenteren. My studies during the period from 1995 to 1999 have resulted in the present thesis.

In 1999 I was appointed as a theoretical ecologist (postdoc) at the Netherlands Institute of Ecology, NIOO-CL, within an EU-funded project on the effects of inducible defences on the functioning of aquatic food webs.

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Vos, M. & Vet, L.E.M. Geographic variation in host acceptance in the parasitoid *Cotesia glomerata*: genotype versus experience.

Vos, M., Burgmans, J.W.H.A. & Vet, L.E.M. Travelling behaviour in the parasitoid *Cotesia glomerata*: a comparison between American and European populations.

Vos, M. & Hemerik, L. Linking foraging behaviour to lifetime reproductive success for an insect parasitoid: adaptation to host distributions.

Schippers, P., Verschoor, A., Vos, M. & Mooij, W.M. Does supersaturated coexistence explain the paradox of the plankton?

Papers in preparation

Lass, S., Vos, M., Spaak, P. Hatching with the enemy: on chemical cues, *Daphnia* diapause and the risk of fish predation.

Vos, M., Verschoor, A., Kooi, B. & Mooij, W.M. Inducible defences: the effects of dynamic interaction strengths on community persistence.

Mooij, W.M., Vos, M. & DeAngelis, D.L. Extinctions in the fast lane: on the evolution of weak trophic interactions

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